Coral Community Dynamics and Disturbance: A Modelling Approach for Caribbean Coral Reefs

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Summary

The capacity of reefs to recover after disturbance is fundamental to prediction of their stability. This is particularly relevant now, following the global decline of reefs during the last decades. A discrete, spatially explicit model (probabilistic cellular automaton) was developed to simulate a Caribbean coral community. Community complexity was generated from behaviour of fundamental units of corals, the polyps. The model includes all known major life history attributes of the corals, based on real data. Structural properties of the model were tested for stability and computational efficiency.

Disturbances of several types were investigated; natural background disturbance, and warming events, both as single and repeated incidents to assess recovery dynamics in the light of ongoing, intensifying climate-mediated global changes.

Regarding background disturbance, area disturbed and patch size were investigated; both were equally important in driving coral community structure and diversity. A powerlaw model was developed to predict natural disturbances, and implemented in later testing of system dynamics. Corals were assigned differential susceptibilities to background disturbances. Results assessed against field data showed that most modelled species had realistic colony size frequency distributions (though 20% had insufficient comparison data).

Following model development, recovery from single impacts (simulated warming events) was tested. Model responses indicate importance of local setting to community resilience. Individual susceptibility of species was mediated by life history strategy investment.

Application of a warming sequence of predicted anomalies for this century was then introduced. Community composition changed between 0-40 years from predominantly persistent, large, slow growing species to small, fecund, fast growing species. After 40 years a phase shift occurred in which algae dominated the community. It is concluded that the future may herald declines in the main Caribbean reef-building species, in ways that match several previous but largely untested speculations. This model indicates that there will be serious implications to reefs, including their numerous commercially important species.

Abbreviations

DHM	Degree heating months
DHW	Degree heating weeks
HadCM3	Hadley Centre Coupled Ocean Atmosphere General Circulation Model 3
HadISST	Hadley Centre Interpolated Sea Surface Temperature Analysis
H'	Shannon Wiener Diversity Index
MMM	Maximum monthly mean climatologically expected SST
PAR	Photosynthetically active radiation
SST	Sea surface Temperature
UVR	Ultra-violet radiation

Chapter 1. Introduction

1.1. Motivation for research

Coral reefs are one of the most valuable and diverse marine ecosystems. Dramatic declines in reef health have been reported from nearly every region where reefs are found (Bryant et al., 1998), and 50-70% of all coral reefs are now under direct threat from human activities (Bryant et al., 1998; Goreau, 1992; Sebens, 1994; Wilkinson and Hodgson, 1999). This section outlines the importance of coral reefs, both in economic terms and intrinsically as sources of biodiversity. It highlights the major threats to reefs today, and in doing so, stresses the urgent need for better prediction of how they respond to an anthropogenically-mediated changing environment. Prediction of coral communities is vital to provide direction and support for their conservation and management, and is the broad motivation for this research.

1.1.1. The importance of coral reefs

Coral reefs rival rainforests in species diversity (supporting 1-9 million species), and greatly exceed them in the number of phyla present (32 out of 33 known) (Reaka-Kudla, 1997). Coral communities are central in constructing the physical and energetic framework of reefs and hence to the maintenance of this high diversity (Sebens, 1994).

Coral reefs are typified by high productivity in otherwise unproductive waters, making them critical to the survival of local people. Although coral reefs are found in 100 countries, most occur in the less economically developed tropical regions. Globally, an estimated 15% of the world's population (0.5 billion people) live within 100 km of coral reef ecosystems and depend in part or entirely on coral reefs for their livelihood (Pomerance, 1999 in Hoegh-Guldberg, 1999).

Reefs provide 25% of the fishery catch in developing countries from less than 0.2% of the world's oceans (Bryant et al., 1998). Annually, fisheries in coral reef ecosystems yield at least six million metric tonnes of fish catches worldwide (Munro,

1996). Fisheries in coral reef areas also have importance beyond the generation of monetary wealth, as they are an essential source of protein for many millions of the world poorest societies (Hoegh-Guldberg, 1999). Thriving reef environments also generate a substantial and growing revenue through tourism, a fast-growing industry sector, which is set to double in the near future. For example, one hundred million tourists visit the Caribbean each year and SCUBA diving in the Caribbean alone is projected to generate almost $US 1 billion by the year 2005 (US Department of State, 1998 in Hoegh-Guldberg, 1999). It is also the primary industry for small island states such as the Maldives (Wilkinson, 2000).

Coral reefs buffer adjacent shorelines by reducing wave action and the impact of storms, erosion and flooding. This is particularly important on low-lying atolls e.g. Maldives (McClanahan et al., 2000). In addition, coral reefs protect mangroves and sea grass beds in some localities, protecting important nursery grounds for commercially important fish species.

Other than fisheries, coral reefs provide locally valuable products from corals and shells made into jewellery and tourism curios, to live fish and corals for the aquarium trade, as well as sand and limestone for the construction industry. However, these extractive activities are usually damaging to reef habitats (Bryant et al., 1998).

The last decade has also seen considerable interest in research and development of marine derived pharmaceutical products. Many of these chemicals originate from coral reef species, whose diversity at organism and metabolic levels has led to the evolution of many complex secondary metabolites, which are being tested in new treatments (Adey et al., 2000; Birkeland, 1997). Corals are also already being used for bone grafts, due to the purity and porosity of the calcium carbonate skeleton. According to one estimate, half of all new cancer drug research now focuses on marine organisms (Bryant et al., 1998).

1.1.2. Current threats facing reefs

Approximately 11% of the world's reefs have been destroyed, having been mined for sand and rock, built on, or buried under sediment from inappropriate land use, and a further 16% are severely damaged and not fully functional (Wilkinson, 2000). Nearly

60% are under threat from human activities (Bryant et al., 1998). Some of the most widespread and severe threats are highlighted below.

1.1.2.1. Coastal development

Sedimentation from dredging and runoff is one of the biggest potential sources of reef degradation in the Caribbean and Pacific (Rogers, 1990; Sheppard, 2002). Dredging for construction has destroyed reefs, associated seagrass beds and mangroves (Bryant et al., 1998; Wilkinson, 2000). (The direct biological impacts of sedimentation are discussed in Section 1.4.2.1). Removal of mangroves for coastal development has also led to increased rates of sedimentation in adjacent reefs (Rogers, 1990). Pressure on reefs from coastal development is predicted to increase in the future with expansion of the world's population, particularly in less developed tropical areas (Wilkinson, 2000).

1.1.2.2. Over-exploitation and destructive fishing practices

Over-fishing increasingly damages reefs worldwide, reducing both abundances and sizes of fish. Subsistence fishing in populous areas can systematically remove all large fish from the reef community e.g. in Jamaica where few large fish remain greater than 30 cm (Sebens, 1994). Herbivore fish species have been sufficiently reduced in some places to change benthic community structure, permitting the proliferation of algae (Hughes, 1994). Blast fishing has severely impacted reefs in places such as South East Asia (Edinger and Browne, 2000; Oakley and Pilcher, 2000).

The value of and demand for reef fisheries products has increased rapidly, particularly for export to East Asia (Wilkinson and Hodgson, 1999). Certain high value species have been selectively removed from reefs, in some areas leading to scarcity, even local extinction e.g. sea urchins, sea cucumbers, giant clams, grouper, turtles, lobsters and queen conch (Birkeland, 1997; Bryant et al., 1998; McClanahan et al., 2000).

The marine ornamental aquarium trade has also created a demand for exotic and colourful reef fish and invertebrates, and has contributed to the decline of diversity in

some areas, e.g. Sri Lanka, where reefs supply about 60% of the US $6.6 million import demand (Wilkinson, 2000).

1.1.2.3. Terrestrial pollution and erosion

Land run-off has many indirect effects such as excessive sedimentation, eutrophication and pesticide pollution. Factors such as forest clearance on adjacent land areas often lead to erosion and flooding, damaging agricultural practices and urban sewage. Impacts on coral reefs are likely to be chronic, but may be episodic, depending on local climatology and oceanography (Andrefouet et al., 2002). Oil pollution has been shown in several cases to have both immediate impacts and severe long-term implications for reef health and recovery (Guzman et al., 1994; Guzman and Holst, 1993; Guzman et al., 1991; Loya, 1976b).

1.1.2.4. Global climate change

Climate is predicted to change globally in ways related to increasing carbon dioxide emissions during the last century and predicted in the next (IPCC, 2001). Some predicted consequences of climate change have serious consequences for future coral reef health. These include increased sea temperature, sea level rise, changes in seawater chemistry leading to decreased calcification of reef organisms and increased frequency and intensity of storms. These are discussed in Section 1.5.

1.1.2.5. Interaction of multiple stressors

Many reefs around the world suffer from complex combinations of stresses, where effects have proved difficult to separate. It is not well known how such impacts interact, both with each other and with ongoing natural disturbances. For example the abundance of algae in many areas of the Caribbean has been linked to both increased nutrient levels and over-fishing (Wilkinson, 2000). In some places the consequences have been dire e.g. Jamaica, where the interaction of hurricane damage, disease, over-fishing and nutrification have reduced coral cover from 62% to 5% in two decades (Hughes and Connell, 1999). Responses to multiple stressors is often unpredictable; the influence of both increased salinity and temperature was less stressful for corals than the sum of the stressors acting independently in Florida Bay (Porter et al., 1999).

Furthermore it is suggested that anthropogenic influences on reefs act to reduce the resilience of coral communities, so they might be less able to recover from future acute impacts. A theoretical model proposed by Gunderson (2000) suggests that the transition of a system between stable states (or stability domains) is mediated by resilience, which can be explained as 'basins of attraction' around domains. This capacity for renewal provides an ecological buffer protecting the system from shifts to alternate stable states. However, reductions in this renewal capacity can lead to serious system changes from disturbances that previously would not have had lasting effects. Anthropogenic activities may operate in this way, reducing buffering capacity of coral reefs by reducing growth rates, survival rates or by interfering with reproduction or settlement processes (see Section 1.4.2.1).

1.1.3. Changing reef management and conservation concerns

Until the late 1990s attention was focussed on conserving and managing reefs through mitigation of local impacts, which were perceived as presenting the biggest threats. At a meeting in 1993[1], Buddemeier stated cynically "*for coral reefs, the major problem with climate change is that it is unlikely to be severe enough to eradicate humans*", illustrating the primary concern for widespread but localised degradation induced by human activities. The overwhelming view at that time was that remote coral reefs remained in near pristine condition while those close to centres of human population were in serious decline. Opinion has changed radically in the wake of the 1998 global bleaching mortality event, with emphasis now expanded to incorporate global effects (this is further discussed in Section 1.5). This came simultaneously with the recognition that even isolated reefs have declined equally e.g. offshore atolls in Belize (McClanahan et al., 2001a) and remote oceanic atolls in the Indian Ocean (Sheppard, 1999).

Issues are beginning to be viewed on extended temporal scales. Historically, reef studies have been carried out on short time scales, with most detailed studies post-dating the widespread use of SCUBA (1960s). This year-decadal view of processes is short compared to the lifespan of many long-lived corals (centuries), and provides only a snapshot perception of long-term processes. As some disturbances and many

[1] Global Aspects of Coral Reefs: Health, Hazards and History, Miami, June 1993 (Roberts, 1993).

resulting trends in coral community structure such as recovery of mature communities, occur over long timescales, the issue of temporal scale is receiving increasing awareness (Connell et al., 1997).

1.2. Addressing these issues

There are several synergistic, additive or competing processes that are leading to a decline in reefs. Given, as noted above, that reefs are vital to many millions of people for provision of protein and structural protection, it is not surprising that questions are increasingly being asked regarding the future of these valuable resources. These questions are approached here using a simulation model. This approach was initiated for reasons outlined below.

The collation and incorporation of species-specific attributes of corals into a mechanistic model allows the current level of understanding of processes structuring communities to be assessed and any gaps in our knowledge to be highlighted.

Processes can be isolated and their influences on model output quantified separately or synergistically with other processes, as permitted by mechanistic nature of the model. This would be difficult, if not impossible to do experimentally.

Influences can be investigated over temporal scales that would not be possible with field studies.

Current understanding of direct biological responses of corals to impacts reported in the literature can be utilized to expand population and community responses (under assumptions derived from published field and laboratory experimentation).

Contemporary climatic predictions can be applied with varying scenarios to modelled coral communities to predict possible future coral communities.

For the present work, a Caribbean coral community is simulated. This was selected primarily because of the low species diversity of this region compared to the Indo-Pacific biogeographical region; many Caribbean reef communities are composed of

<20 scleractinian species (Goreau, 1959). These communities are amongst the best studied in the world, with records spanning four decades for some areas (e.g. Jamaica, Goreau, 1992). The taxonomy of these corals is relatively well understood in comparison to Indo-Pacific corals, and many aspects of their biology have been established (e.g. reproductive strategies, Szmant, 1986, and dynamics along environmental gradients such as depth, Bak and Luckhurst, 1980; Bak and Nieuwland, 1995, and wave exposure Geister, 1977; Witman, 1992). This means that corals can, for the most part, be modelled at species level, without the necessity to artificially categorise them into functional groups thereby decreasing the resolution of the model output, and information is available on which to base parameters.

Full details of model selection and application to coral population and community dynamics are given in Chapter 2.

1.3. Organisational levels of corals

An individual coral can be viewed on three levels; polyps, colonies and genetic individuals. This section reviews aspects of coral biology, taking a 'bottom up' approach to organisational levels, and highlights processes acting on each level to shape coral populations and communities which are relevant to the coral community model.

1.3.1. Coral polyps

"*Intricately organised and immensely diverse, the living coral reef is the triumphant achievement of coral polyps...*" (Veron, 1986).

Coral polyps are morphological individuals; each has the same basic structure including a mouth and gastric cavity. Polyps can live as single units i.e. following settlement from the plankton, however mostly they are connected to one another by tissue. Polyps bud, either by extratentacular (new polyps developing between existing ones) or intratentacular (binary fission) mechanisms. Once budded off, they remain connected to their sister polyps by a layer of tissue and can exchange nutrients. Polyps stop growing once they reach a particular size characterised by the species, indicating genetic controls on polyp growth. However, considerable

plasticity can be shown in skeletal structure and polyp spacing. Most corals are both hetero- and autotrophic, containing symbiotic dinoflagellate algae, zooxanthellae, inside their gastrodermal cells. This tightly controlled relationship with algae is vital both for nutrition and calcification in the coral host (Barnes and Chalker, 1990).

1.3.2. Coral colonies

Coral colonies have a coordinated colony shape and display varying degrees of functional specialisation of polyps in that parts of the colony may be specialised for reproduction (central areas) or defence (edges) (Hall and Hughes, 1996).

1.3.2.1. Indeterminate growth

As modular organisms, coral colonies are considered to have indeterminate growth (Sebens, 1987), though colony architecture may also be modified by competition and partial mortality. There is no evidence to suggest absolute growth rates (as radial extension rates) change with colony size or age (Connell, 1973; Hughes and Jackson, 1985; van Moorsel, 1985), though relative growth rates decline with increasing colony surface area or volume.

1.3.2.2. Morphotypic plasticity

The growth form of coral colonies is extremely plastic. Coral colony morphology within a species is influenced by both light level (Grassle, 1973) and wave energy (Geister, 1977). Chappell (1980) predicted increased branching with increasing light levels, and less branching with increasing hydrodynamic stress, as an adaptation towards increased structural strength. He also predicted morphology would change with sedimentation regime, to intercept the smallest proportion of settling sediment per unit surface area (i.e. columnar rather than plating), and with sub-aerial exposure, where forms would minimise surface to volume ratio to minimise water loss as well as spreading sideways (i.e. mound-shaped and encrusting growth forms).

1.3.2.3. Size structured populations

Most coral populations consist of predominately small colonies with comparatively few large ones (Bak and Meesters, 1998; Hughes and Jackson, 1985; Soong, 1993). While small corals are numerically most abundant, they generally constitute a small proportion of the total cover of live coral; e.g. more than half of all colonies from

five species of foliaceous corals fell into the smallest size class of 1-10 cm, but accounted for ~5% of the coral cover (Hughes and Jackson, 1980). Equally, Meesters et al. (2001) found that the largest 5% of colonies represented over a third of total colony surface area. The size structure of coral populations is stable across temporal (Hughes and Jackson, 1985) and spatial scales (Meesters et al., 2001; Soong, 1993), and is highly species specific (Meesters et al., 2001). But populations are extremely dynamic; individual colonies are highly mobile, both demographically (transitions between size classes, Hughes and Jackson, 1985) and spatially (across substrata, Bak and Luckhurst, 1980). As a consequence of clonality, coral colonies undergo complex mortality processes: shrinkage (negative growth), fission, and total colony death. These processes distort the relationship between age and size in all but the smallest corals (Bak and Meesters, 1998; Hughes and Jackson, 1980; Miller et al., 2000).

Colony shrinkage

Colony shrinkage is brought about by partial mortality. Partial mortality processes are more important than total colony mortality in some coral species e.g. *Montastraea annularis* and *Agaricia lamarcki*, accounting for a greater proportion of dead coral tissue than total colony death (Hughes and Jackson, 1985). Colony shrinkage has strong implications for size-dependant life history processes i.e. colony mortality rates and fecundity.

Colony fission

Colony fission occurs by three mechanisms: 1) death of part of a colony leaving two or more clones sharing a common skeleton, 2) colony fragmentation via skeletal breakage or 3) by specialised morphological structures such as polyp balls (Rosen and Taylor, 1969). The first two mechanisms are uncontrolled by the coral, as a direct result of disturbance impacts, and are always associated with loss of tissue. The latter constitutes asexual reproduction, i.e. an adaptive mechanism to replicate the colony and colonise new areas (Sheppard, 1981). In certain species, notably Acroporiids that live in high wave energy environments at the top of Caribbean fore reef slopes, fragmentation is an important part of asexual reproduction (Highsmith, 1982). Fragile skeletons (Tunnicliffe, 1979) and rapid rates of growth and tissue regeneration (Bak, 1983) combined with very low recruitment rates for sexually produced juveniles (Tunnicliffe, 1979), indicate that fragmentation is a fundamental

process in the life history of these corals, and the primary mode for maintenance and dispersal of populations (Highsmith, 1982).

The importance of colony fission in maintaining populations is likely to vary with species, but even in corals with high larval recruitment rates e.g. *Agaricia* spp., this process can account for more than twice as much 'recruitment' than settlement and survival of sexually produced larvae (Hughes and Jackson, 1985).

Colony fusion

A coral colony separated into different physical entities has the potential to fuse again at a later date. This is especially prevalent in situations where previously separated colonies continue to live on a common skeleton and, in time, regenerate lost tissue between each part. Frequencies of colony fusion vary with species and colony growth form. For example Hughes and Jackson (1985) found highest rates of fusion in the robust, sheet-forming Agariciid, *A. lamarcki* (4-6% of the population per year), and lowest in the fragile saucer coral *Leptoseris cucullata* (0.9-3.6%). Importantly, fused colonies had a high survival rate, an advantage of suddenly increasing net size.

Allogenic fusion of corals of distinct genotypes is also known to occur, primarily in newly settled juveniles (van Moorsel, 1985), where the sudden increase in size (and decreased probability of death, see below) offsets the cost of competition for shared resources (Hidaka, 1985). Adult colonies can also fuse, though the capacity to do so varies with species. The frequency of chimeras in the field is not known, neither are the consequences on colony survivorship associated with allogenic fusion processes (Hughes et al., 1992). Such colony formation is also likely to have wider biogeographic and evolutionary implications (Veron, 2000).

1.3.2.4. Size related mortality

The relative importance of total colony mortality (death) versus partial mortality (shrinkage) is closely related to colony size. Small corals either die outright or escape mortality (Hughes and Jackson, 1980). Connell (1973) suggested that survivorship of small colonies is low because of their poor ability to recover from injuries. He hypothesised that smaller colonies have fewer reserves of energy or materials to

transfer from undamaged polyps for repairing wounds. Thus regeneration should be slower and less successful, leading ultimately to complete mortality of the colony. Small colonies are also likely to be more susceptible to instant whole colony mortality from the activities of grazers or smothering by sedimentation (Bak and Engel, 1979; Birkeland, 1977; Rylaarsdam, 1983; Sammarco, 1980). Whole colony mortality is rare in intermediate and large colonies compared to those <10 cm diameter for *Montastraea annularis* (Bythell et al., 1993b)

Partial mortality also increases with colony size (Bythell et al., 1993b; Meesters et al., 1997). The amount of surface area of coral colonies affected by partial mortality also increases with colony size (Lewis, 1997). In the largest size classes of a population, partial mortality reached values of 30-50% of colony surface area (Meesters et al., 1997). Levels of partial mortality are highly variable between species. This is a function of the regenerative capacity of coral species to repair lost tissue (Meesters et al., 2001), which is highly variable between species (Bak, 1983; Bak and Steward van Es, 1980).

1.3.2.5. Constraint of colony size on reproduction

The onset and continued capacity for sexual reproduction and fecundity of corals is also related to colony size. Corals have a minimum threshold size above which they are fecund (Soong, 1993), suggesting that resources are initially directed towards colony growth to escape the high risk of mortality experienced by small corals. Size of first reproduction varies with species, and is positively correlated with adult size (Soong, 1993; van Moorsel, 1983)[2]. Reductions in size to below the threshold reproductive size e.g. colony shrinkage via partial mortality, leads to diminished output or complete loss of fecundity (Hughes et al., 1992; Szmant-Froelich, 1985a; Zakai et al., 2000). Finally, net fecundity is strongly correlated to colony size as the largest individuals in a population make greatest contribution to the gene pool, though numerically they constitute a small proportion of the population. For example Babcock (1984) found that 25% of larvae originated from the largest 3% of colonies in a population of *Goniastrea aspera*. Also fecundity has the potential to rise indefinitely if growth is undisturbed, with the indeterminate addition of gravid

[2] There also seems to be a relationship between adult colony size and reproductive mode (see Section 1.4.1).

polyps (Hall and Hughes, 1996). Furthermore, large colonies are immune to many sources of whole colony mortality, and are likely to repeatedly breed, while small colonies may reproduce only once (Hughes et al., 1992).

1.3.3. Genetic individuals

1.3.3.1. Genetic recombination: sexual reproduction.

Although early work indicated that corals primarily brood their embryos prior to release (planulation), more recent studies have shown that corals have diverse modes of sexual reproduction (Harrison et al., 1984). Species vary in terms of sex, mode of embryonic development (i.e. internal brooding of embryos or planktonic embryonic development) and number of reproductive cycles per year (Szmant, 1986). In Caribbean corals there is a relationship between the latter two traits: brooding species mostly have more than one reproductive cycle per year e.g. *Favia fragum, Porites astreoides* and *Agaricia* spp. (Szmant, 1986; van Moorsel, 1983), while broadcast spawning species generally reproduce once each year e.g. *Montastraea annularis, M. cavernosa, Siderastrea siderea, Diploria strigosa, Acropora cervicornis* and *A. palmata* (Szmant, 1986). Mode of reproduction also correlates with colony size and can be regarded as adaptive to a certain life history strategy (this is further discussed in Section 1.4.1). Reproductive mode determines the dispersive capacity of a species, and hence can influence recovery following disturbances.

A further mechanism exists in a limited number of corals, namely parthenogenesis, or the brooding of clonal larvae (Babcock, 1984). This is interesting from an evolutionary viewpoint, but does not constitute sexual reproduction, though it may be important in maintaining populations at low densities (i.e. following severe disturbances) (Knowlton, 2001).

1.3.3.2. Evolutionary consequences of clonality

Clonality enables genetic individuals to spread the risk of mortality across several physiologically discrete units. Due to their modularity, corals can survive severe disturbances that would prove fatal to aclonal organisms that cannot generally survive large amounts of injury. Hence corals can be extremely long-lived, and are likely to have low rates of genetic turnover. For example *Montastraea annularis*,

where recruitment from sexual reproduction is virtually non-existent, is one of the most common Caribbean corals (Bak and Engel, 1979; Hughes and Jackson, 1985; Hughes and Tanner, 2000; Rylaarsdam, 1983). However, once a genotype with a selective advantage appears, this can be rapidly cloned, and potentially swamp the reproductive output of a population after only a single generation (Lasker and Coffroth, 1999). Clonality can reduce genetic diversity when high numbers of ramets inhibit settlement of sexual recruits (recruitment in corals is considered to be space limited (Muko et al., 2001a; Roughgarden et al., 1985)). But if density dependence of larval stages is absent, clonality will only affect the size of genetic individuals, not the number present (Lasker and Coffroth, 1999). The most successful genetic individuals (i.e. the ones with the largest colonies) have disproportionately high fecundity, potentially further decreasing genetic diversity.

1.4. Coral community dynamics

1.4.1. Life history strategies of Caribbean corals

Corals vary in their life history strategies; some are fecund, fast growing and short-lived, while others are highly persistent (Hughes and Jackson, 1985). Resources are differentially invested into a suite of traits (e.g. mode of reproduction, recruitment, growth and skeletal form, competitive ability and rates of tissue regeneration following damage). Individual life history strategies result from the summation and integration of these traits (Hughes et al., 1992).

In Caribbean corals, brooding is associated with small-sized species, while broadcast spawning is prevalent in species with large colonies (Szmant, 1986). Since colony growth is indeterminate, small size implies either that colonies have low survival or they lack the capacity to regenerate lost tissue. In the case of corals such as *Agaricia agaricites* both of the above appear to be true (Bak, 1983; Bak and Engel, 1979; Bak and Luckhurst, 1980). But nurturing embryos until planular stage does confer relatively high recruitment success (Bak, 1983; Hughes, 1985; Rylaarsdam, 1983). Thus such species are able to persist in less stable environments through high rates of population turnover (Bak and Luckhurst, 1980; Hughes and Jackson, 1985). The

skeletons of these ephemeral species are often fragile, indicating low investment, thus dislodgement and breakage are common, leading to high spatial mobility across the substratum (Bak and Luckhurst, 1980). Mobility is also enhanced by relatively high rates of growth (Hughes and Jackson, 1985) and low competitive ability (Lang, 1971; Logan, 1984); competitive contests for space are repeatedly lost, but parts of colonies survive through growth directed away from competitors (Hughes and Jackson, 1985).

Large-sized species generally have robust skeletons and are frequently intermediate to high-ranking competitors (Lang, 1971; Logan, 1984), and are also relatively efficient at repairing tissue lesions, e.g. *Montastraea annularis* (Bak, 1983). Such corals can maintain their colony integrity and attain large sizes. They can be long-lived, but the costs of colony maintenance are offset by delayed reproduction and relatively slow growth rates (Hughes et al., 1992). Their lower recruitment success is compensated for by repeated reproduction throughout their long lifetimes.

Mortality has different effects on species according to their individual life histories. Bak and Luckhurst (1980) found that total colony mortality in large colonies (>30 cm diameter) was highest for *Agaricia agaricites* and *Meandrina meandrites,* but relatively low in *Montastraea annularis, M. cavernosa* and *Agaricia lamarcki* in Curaçao. This may be partly related to colony morphology (i.e. robust structures can better resist disturbances than very fragile branching or plating growth forms), or overall size of colonies (very large colonies are considered to be immune to many natural forms of disturbance). At a population level, species have different responses to changes in life history processes (Hughes and Tanner, 2000). Findings from a simulation study indicated that populations of *Agaricia agaricites* and *Leptoseris cucullata* were strongly influenced by declines in recruitment, while *Montastraea annularis* was most affected by changes in survival (Hughes and Tanner, 2000).

The concept of life history strategies has been taken further by Bak and Meesters (1997), to examine questions regarding ecosystem functioning, diversity and identification of keystone species through grouping species with similar effects in key ecosystem processes such as recruitment and calcification.

1.4.2. Processes structuring coral communities

Variability in community structure is a striking feature of marine environments (Levin, 1992), so it can be difficult to identify the processes driving these patterns. Coral reefs provide numerous examples of spatio-temporal variation (Aronson and Precht, 2000; Hughes et al., 1999; Karlson and Cornell, 1998). For example, coral reefs with high cover and species richness are often interspersed with areas of reduced coral cover, and profound changes in community structure can occur on a time scale of decades (Knowlton, 1992). Such patterns are a result of differences in habitat and substratum type, as well as the history of physical and biological phenomena affecting communities (Connell, 1978; Hughes, 1989; Rogers, 1993).

1.4.2.1. Disturbance

Disturbance has been defined as any process that clears primary substratum (Sebens, 1994) or damages and kills residents (i.e. corals) (Connell, 1997). Disturbance opens up space or resets a patch of substratum to an earlier successional stage. Without significant disturbance, each depth zone of a reef could theoretically become dominated by a single coral species able to out-compete all others. Any reef, at any given time, comprises a set of patches of substratum at different stages of recovery from small to large disturbances. The term equilibrium has been frequently used to denote the climax or undisturbed community state. The actual equilibrium coral community, however, is a landscape of all successional stages, for a given pattern and rate of disturbance over time; it is a temporal mosaic (*sensu* Grassle, 1973). Thus coral communities are defined as non-equilibrium communities (Connell, 1978; Karlson, 1999; Pearson, 1981; Tanner et al., 1994). Of the various hypotheses put forward to explain these dynamics, the most widely accepted is the intermediate disturbance hypothesis (Connell, 1978), but since its proposal, the roles of recruitment dynamics and reef connectivity have also been recognised (Lewin, 1986; Roberts, 1997).

Natural disturbance

Natural disturbances can be physical (sedimentation, sand scouring, aerial exposure, dislodgement and breakage) or biological (predation, competition, disease, and the activities of boring organisms). Natural disturbances vary widely in spatial and temporal scale, from frequent small openings (i.e. predation) to rare events when

large areas are cleared (i.e. hurricanes, extreme low tides). These can constitute a significant structuring force.

Gradients of natural disturbance exist with depth, exposure and light attenuation (Huston, 1985). Patterns of zonation (Goreau, 1959; Graus and Macintyre, 1989; Graus et al., 1984), species diversity (Sheppard, 1982) and persistence (Bak and Luckhurst, 1980) are attributed to such gradients.

Storms and hurricanes are acute natural stressors. Their effects on coral communities are highly spatially variable (Bythell et al., 1993a; Rogers, 1993). Most impacts are through physical damage to corals, but this is often species selective. Some growth forms are more resistant to hurricane impacts than others (Woodley et al., 1981), thus such disturbances can induce changes in the structure of coral communities (Bythell et al., 1993a). Hurricanes also alter the physical environment e.g. Heron Island, where water flow patterns were modified and corals became exposed to air for longer periods (Connell et al., 1997). The severity of hurricane impacts in part depends on the history of a particular community, i.e. the period of time since the previous hurricane (Hughes and Connell, 1999).

Predation can also control coral distribution. Episodes of large scale predation e.g. crown of thorns starfish, *Acanthaster planci*, across the Great Barrier Reef received significant attention during 1970s and 1980s (Colgan, 1987; Done, 1992; Endean et al., 1988), as have outbreaks of the corallivorus gastropod *Drupella cornus* (Turner, 1994). Reefs experience low-level predation by some fish and invertebrates such as parrotfish, butterflyfish, nudibranchs and worms (e.g. *Hermodice* spp.). This can have a strong influence on the community structure of corals (Neudecker, 1979). Damselfish can also influence the structure of coral communities by selectively gardening certain algal species and removing juvenile corals (Gleason, 1996; Wellington, 1982). Skeletal-boring organisms weaken coral skeletons making them more susceptible to dislodgement and fragmentation (Tunnicliffe, 1979).

Anthropogenic disturbance

Many recent and damaging disturbances originate from anthropogenic activities. These can be acute but are more often chronic in nature (Connell, 1997). Some

agents simply remove corals by killing them, but many effects such as sedimentation and pollution, make the environment less favourable for recolonisation by corals and/or interfere with coral physiology (Dubinsky and Stambler, 1996). These sublethal effects have increasing implications for reef recovery (Connell, 1997).

Sedimentation and eutrophication are two of the most widespread human induced disturbances affecting coral reefs (Roberts, 1993). Sedimentation is generally a chronic disturbance. Sediment in the water column decreases light availability for photosynthesis, thus decreasing rates of coral growth (Rice and Hunter, 1992). Sediments settling onto substrata can inhibit coral settlement, reduce juvenile survival, and require energy expenditure for mucus production for sediment rejection (Rogers, 1990). Corals exposed to high sedimentation often differ markedly from those with low rates of sedimentation in terms of both their community structure (Loya, 1976a; Rice and Hunter, 1992) and colony morphology (Chappell, 1980). Coral species differ in their resistance to sedimentation, a feature tentatively linked to polyp size (Rogers, 1990). Sometimes coral colonies are larger in heavily sedimented areas, indicating low recruitment (e.g. Cortes and Risk 1984, Maragos 1974, Brown et al. 1986 in Rogers, 1990) but in other places corals appear to be smaller, indicating decreased rates of survival and increased rates of partial mortality (Loya, 1976a).

Increased nutrient levels can have serious and complex consequences. This often comes about through sewage pollution and runoff from agriculture. Increased nutrient availability enhances algal growth, particularly that of competing fleshy macro algae (Hughes, 1994; McCook, 1999). This may shift the balance of competition, which can lead to phase-shifts from a coral dominated to algal dominated community (Done, 1992; McCook, 1999; Miller, 1988).

1.4.2.2. Supply-side ecology

The variable supply of new individuals affects adult populations (Lewin, 1986). Although most populations have some level of immigration, this is particularly important to open marine populations where local recruitment is largely uncoupled from local reproduction by a dispersive larval phase (Caley et al., 1996). The supply of recruits is fundamental to the genetic structure of populations, population dynamics and community structure (Connell and Keough, 1985; Lewin, 1986).

The last fifteen years has seen increased interest in this area, after early assumptions were dispelled that benthic marine communities were saturated with recruits (i.e. changes in supply would not influence adult community structure) (Roughgarden et al., 1985). Evidence from temperate systems has shown that relative importance of the recruitment signal increases with decreasing spatial occupancy, from field (Connell, 1985) and modelling studies (Gaines and Roughgarden, 1985).

Little is known about the fate of gametes after release (Caley et al., 1996), though most eggs are buoyant and thus may be concentrated and/or retained by water flow patterns (Black et al., 1991; Szmant-Froelich, 1985b). The length of larval competency periods in the plankton, which also spatially constrains dispersal, varies with mode of embryonic development; coral larvae settle typically between 2-3 days from release for brooding species and 5-10 days from release for broadcast spawning species (Harrison and Wallace, 1990). Coral larvae actively select a site for settlement, responding to environmental cues, such as substratum topography (Carleton and Sammarco, 1987), orientation (Baggitt and Bright, 1985) and condition i.e. presence of coralline algae (Pearson, 1981; Raimondi and Morse, 2000; van Moorsel, 1989). This behaviour can explain patterns of recruitment to some extent, particularly in brooding species where there is evidence for settlement aggregations (Carlon and Olson, 1993; Lewis, 1970).

Rates of recruitment are highly variable, both spatially, and temporally (Hughes et al., 2000; Wallace, 1985). In a study by Hughes et al. (2000), recruitment variability was explained mostly by adult fecundity (72%), and no other variable (reef sector, reef area, abundance of adults or year) contributed significantly to variation in recruitment rates. Reefs act as sources or sinks for coral recruits and this is related to both the degree of connectivity of reefs and larval duration, which also determines levels of self-seeding (Preece and Johnson, 1993; Roberts, 1997). Due to difficulties in determining sources of larvae arriving at reefs, few experimental studies of this nature have been done, but reef connectivity is emerging as an important factor in reef conservation and management (Roberts, 1997).

In the Caribbean, rates of recruitment for broadcast spawning species are much lower than those for brooding species (Baggitt and Bright, 1985; Bak and Engel, 1979; Edmunds, 2000; Miller et al., 2000; Rylaarsdam, 1983; Smith, 1992). This is attributed to post-spawning events in the water column such as reduced embryonic viability or high mortality during the relatively lengthy larval planktonic duration (Szmant, 1991)

1.4.2.3. Post-settlement mortality

Abundance patterns of recruits are often markedly different from adult populations, but, immediate post-settlement processes, which are very important in the development of temperate communities, have only been addressed explicitly in a few cases (Bak and Engel, 1979; Edmunds, 2000; Harriott, 1985; Rylaarsdam, 1983; Sammarco, 1991). Results from the Great Barrier Reef indicate that density-dependent post-recruitment mortality has a 'smoothing' effect on initial spatial differences in recruitment. Initially high rates of recruitment always suffered high rates of mortality, at least in Acroporiid corals (Dunstan and Johnson, 1998).

Species-specific susceptibility of juveniles to disturbances may be related to the ability to recover after disturbances or morphological characteristics. For example, colony elevation above the substratum reduces risk of submergence in sediments or overgrowth by encrusting organisms, (van Moorsel, 1985). Other authors have suggested small-scale spatial differences can be attributed to spatial competition of recently settled coral spat with other sessile organisms (Bak and Engel, 1979; Dunstan and Johnson, 1998) or adult corals (Fearon and Cameron, 1997), fish predation (Miller et al., 2000), or disturbance from grazers (Sammarco, 1980; Sammarco, 1991).

The relative importance of recruitment processes versus post-settlement processes in structuring coral communities is thought to differ with localised environmental factors (Sammarco, 1991), and spatial occupancy. Post-settlement mortality becomes increasingly important at high densities (Connell, 1985; Gaines and Roughgarden, 1985). However, in the Caribbean, rates of recruitment are low in comparison to the Indo-Pacific (Sammarco, 1985; Smith, 1992; Szmant-Froelich, 1985b), yet in many areas abundances of recruits and adult corals are disparate (Bak and Engel, 1979;

Miller et al., 2000; Rylaarsdam, 1983), and some sites showed no evidence for density-dependant juvenile mortality (Edmunds, 2000).

1.4.2.4. Competition

As adult corals are sessile, maintaining space on the reef is of primary importance to their survival. Competitive ability may also have a role in determining the structure and composition of coral communities (Karlson, 1999; Lang and Chornesky, 1990).

Interspecific coral interactions

Mechanisms for spatial competition between corals have been well described (Lang and Chornesky, 1990). Competition is clearly important at individual colony level, as the development and/or deployment of specialised structures for competition is costly and compromises growth and fecundity (Rinkevich and Loya, 1985; Romano, 1990; Tanner, 1992; Tanner, 1995; Tanner, 1997). It has been argued that such interactions should be regarded as defensive rather than offensive, i.e. concerned with colony maintenance rather than overt aggression (Cope, 1981).

The importance of competition in structuring coral communities, however, is not clear (Bak et al., 1982; Bradbury and Young, 1981; Connell, 1976; Licuanan and Bakus, 1992; Sheppard, 1979). Frequencies of observed interactions can be low (Hughes, 1985) or extremely high (Sheppard, 1985b) and appear, at least in some locations, to be correlated with coral density (Logan, 1984). Additional factors can mediate outcomes, making dominance predictions difficult (Bak et al., 1982). Methodological differences in addressing the importance of competitive interactions may in part explain differences of opinion regarding their relative importance; specifically spatial scale (Sheppard, 1985b), and timing can influence results, and repeated reversals in outcome can occur as well as periods where there is no evidence of interaction (Bak et al., 1982; Chornesky, 1989).

A feature of coral competition highlighted by Sheppard (1985b) is the maintenance of unoccupied space around coral colonies. This varies with coral species, but the interactive reach of some corals (*sensu* Sheppard, 1985a) can be as much as 10 cm wide. This space is maintained by specialised mechanisms for competition by corals,

and may not be available for recruitment, thus adult density may mediate rates of juvenile survival (Sheppard, 1985b).

Competitive hierarchies have been constructed for Western Atlantic coral species, from both field observations and experimental manipulations (Lang, 1971; Lang, 1973; Logan, 1984). The most aggressive corals in the Caribbean belong to the Mussidae, and generally form small colonies at low densities e.g. *Scolymia* spp., while most intermediate-ranking corals form large colonies (e.g. *Montastraea* spp.) and subordinate species often have small colonies e.g. *Agaricia* and *Porites* spp. (Lang, 1973; Logan, 1984).

Interactions between corals and algae

The mechanisms and outcomes of competition between corals and algae are poorly understood (McCook, 1999; McCook et al., 2001), even though algae can displace corals (Done, 1992; Goreau, 1992; Hughes, 1994; McCook, 1999; Miller, 1988). Experimental evidence indicates that competition with algae can inhibit the growth or survival of established hard corals (Hughes, 1989; Jompa and McCook, 2002; Miller and Hay, 1996; Potts, 1977; Tanner, 1995) and of coral recruits (Bak and Engel, 1979; Birkeland, 1977; Hughes, 1989; Hughes, 1996; Miller and Hay, 1996). Corals can be harmed by direct contact, overgrowth, abrasion and shading (Coyer et al., 1993; De Nys et al., 1991; Hughes, 1994; Jompa and McCook, 2002; McCook, 2001; Miller and Hay, 1996; Tanner, 1995). Further evidence for coral-algal competition comes from herbivore exclusion studies in which coral cover declined, apparently in response to increased algal abundance (Lirman, 2001; Sammarco, 1982), and following the die-off of the major Caribbean herbivore, *Diadema antillarum* (de Ruyter van Steveninck and Bak, 1986; Edmunds and Carpenter, 2001). On the other hand, corals may competitively inhibit macroalgal growth (de Ruyter van Steveninck et al., 1988), algae can protect corals from bleaching (Jompa and McCook, 1998) and coralline algae can induce settlement of coral larvae (Heyward and Negri, 1999).

Coral and algal community states are mediated by nutrient availability and/or grazer densities, so changes in either of these factors can shift the balance of competition towards an algal dominated state (Aronson and Precht, 2000; Edmunds and

Carpenter, 2001; Jompa and McCook, 2002; McClanahan et al., 2001a; McClanahan et al., 2001b). Algae commonly flourish after a severe disturbance event, and pre-empt space, limiting coral recovery as a result (Connell et al., 1997; Goreau, 1992; Hughes, 1989; McClanahan et al., 2001b; Ostrander et al., 2000; Rogers, 1993; Shulman and Robertson, 1996). Attention is now shifting to encompass wider issues of fisheries and watershed management, due to their implications for coral/algal abundance and reef state (McCook, 1999).

Interactions between corals and other sessile reef organisms

There are very few reports of competition between corals and other sessile reef organisms, even though sponges, ascidians, bryozoans, soft corals, corallimorpharians and anemones can occupy significant proportions of the reef (Karlson, 1980; Reichelt et al., 1986). These organisms compete with corals using both direct and allelopathic mechanisms (Engel and Pawlik, 2000; Langmead and Chadwick-Furman, 1999) (possibly the cause of 'stand-offs' observed by Karlson, 1980) between corals and zoanthids), as many possess complex secondary metabolites, many of which are currently under investigation by pharmaceutical companies for development in medical applications (Bryant et al., 1998). Competition between corals and sponges has been reported (Aerts, 1998), particularly in stressed communities (Aerts and van Soest, 1997; Antonius and Ballesteros, 1998).

1.5. Impacts of climate change on corals

1.5.1. Climate change and predicted scenarios

In recent years, a new threat to coral reefs has been recognised, whose effects may be overwhelming, as global mean temperatures are increasing at unprecedented rates. This is a response to increased radiative forcing due to greenhouse gases. The Intergovernmental Panel on Climate Change (IPCC) has defined 40 future scenarios (SRES[3]), split into four main families (Table 1.1) based on economic, demographic and technological driving forces for future greenhouse gas and sulphur emissions

[3] Special Report on Emissions Scenarios accepted by Working Group III in March 2000 (IPCC, 2001).

which are used to base future predictions on greenhouse gas emissions and consequent climate change (IPCC, 2001), (Figure 1.1). These update and replace earlier IS92 scenarios (IPCC, 1992; IPCC, 1996).

The overall result is that the current rate of temperature increase is unprecedented (Figure 1.1). Warming at the end of the last glaciation was about 1°C per thousand years (Pittock. 1999). Over the last century, warming has been about 0.5°C. Projected warming for the next 100 years is in the range of 2 to 5°C (IPCC, 2001). Clearly the current and predicted rate of warming is much greater than previous levels, raising the question of whether corals can adapt to this rapid rate of change (this is addressed in Section 1.5.5).

Recent behaviour of El Niño Southern Oscillation (ENSO), with a long sequence of El Niño events in the 1990s, has led to controversy as to whether this is part of the normal ENSO inter-decadal variability, or due, in part, to global warming. There is uncertainty due to insufficient records on whether ENSO is moving towards an El Niño dominated mode (see review by Pittock, 1999).

Table 1.1. SRES scenarios, main families and sub-families. Outline of major demographic, technological and economic characteristics (IPCC, 2001). This provides a key for Figure 1.1.

Scenario family	Global population	Global economic diversity	Technological change	Economic growth
A1 - Regional convergence and capacity building:				
	Mid-century peak	Homogeneous, regional convergence	Rapid introduction of new, efficient technologies	Very rapid
Variations A1FI fossil fuel intensive A1T non fossil fuel intensive A1B balanced energy sources				
A2 - Self reliance and preservation of local identities				
	Continuously increasing	Very heterogeneous, regional diversity	Slow and fragmented	Regionally orientated
B1 - Global solutions to economic, social and environmental sustainability				
	Mid-century peak	Homogeneous	Rapid towards clean and resource efficient technologies	Rapid towards information and services
B2 - Local solutions to economic, social and environmental sustainability				
	Continuously increasing (lower than A2)	Heterogeneous	Slow and diverse	Intermediate economic growth

A particularly severe El Niño was experienced globally in 1998, and climatic repercussions included an unprecedented elevation in sea surface temperature (SST) (Wilkinson and Hodgson, 1999). What followed was the most serious coral bleaching and mortality ever recorded, which killed >90% of corals in many Indian Ocean archipelagos.

In response to this and previous regional warming events, research has been focussed on providing ways of classifying anomalous sea temperatures and predicting immediate coral reef responses in terms of bleaching severity and defining thresholds above which bleaching is expected[4].

[4] http://orbit-net.nesdis.noaa.gov/orad/coral_bleaching_index.html.

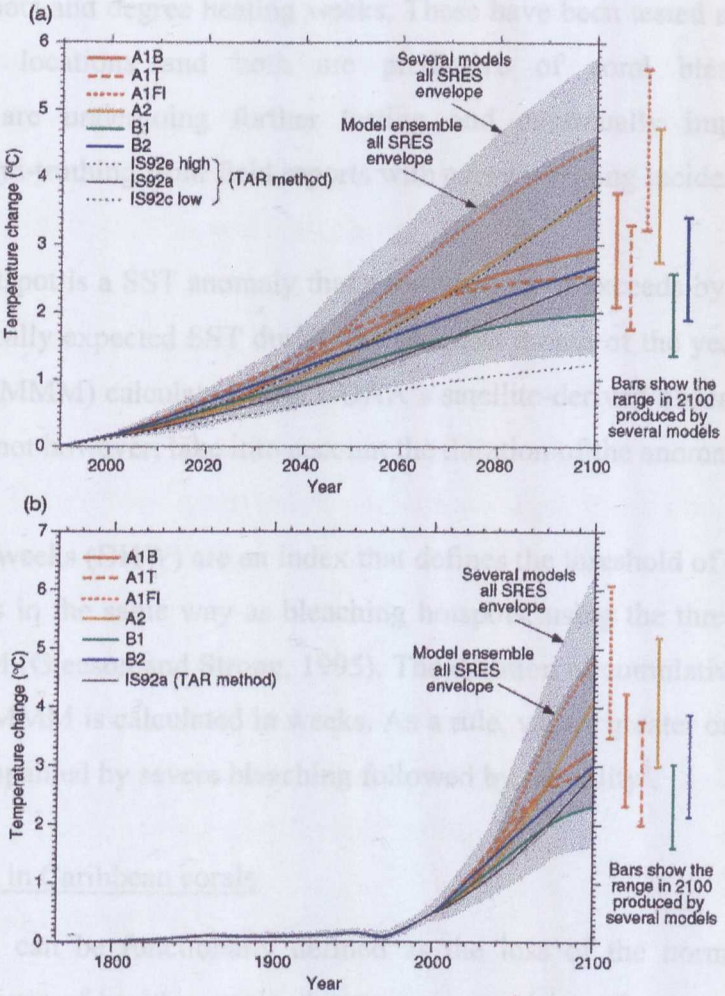


Figure 1.1. (a) Global mean temperature projections for six illustrative SRES scenarios using a simple climate model (details in Table 1.1). Also for comparison, following the same method, results are shown for IS92a. The darker shading represents the envelope of the full set of thirty-five SRES scenarios using average model results (mean climate sensitivity is 2.8°C). The lighter shading is the envelope based on all seven model projections (with climate sensitivity in the range 1.7 to 4.2°C). The bars show, for each of the six illustrative SRES scenarios, the range of simple model results in 2100 for the seven AOGCM model tunings. (b) Same as (a) but results using estimated historical anthropogenic forcing are also used.(Source: IPCC, 2001).

Two methods of classifying anomalous sea temperature have been developed: bleaching hotspots and degree heating weeks. These have been tested against results from multiple locations and both are predictive of coral bleaching. Both classifications are undergoing further testing and continually improving with additional ground-truthing from field reports with every warming incident.

A bleaching hotspot is a SST anomaly that approximates or exceeds by 1°C or more the climatologically expected SST during the warmest month of the year (maximum monthly mean MMM) calculated from NOAA's satellite-derived observations. This technique does not however, take into account the duration of the anomaly.

Degree heating weeks (DHW) are an index that defines the threshold of coral heating at different sites in the same way as bleaching hotspots, using the threshold of 1°C above the MMM (Gleeson and Strong, 1995). The duration of cumulative increase in SST above the MMM is calculated in weeks. As a rule, values greater or equal to ten DHW are accompanied by severe bleaching followed by mortality[5].

1.5.2. Bleaching in Caribbean corals

Coral bleaching can be functionally defined as the loss of the normal brownish colour characteristic of healthy corals, due to mass expulsion of zooxanthellae from coral tissues and/or the decrease in photosynthetic pigments within individual zooxanthella (Hoegh-Guldberg, 1999). It is a response of corals to a range of environmental stressors e.g. cold (Jokiel and Coles, 1977), increased or decreased light (Hoegh-Guldberg and Smith, 1989), low tides, reduced salinity, sedimentation and pollution (Brown, 1997). Most attention recently has been focussed on bleaching in response to increased sea temperature (Glynn, 1996; Hoegh-Guldberg, 1999; Wilkinson and Hodgson, 1999).

Bleaching may occur at local scales (e.g. parts of reefs, Goreau, 1992) or at geographic scales that may involve whole reef systems (e.g. mass bleaching, Glynn, 1996; Goreau, 1992; Hoegh-Guldberg, 1999; Wilkinson and Hodgson, 1999 and

[5] http://www.osdpd.noaa.gov/PSB/EPS/method.html.

Williams and Bunkley-Williams, 1988). Most evidence indicates that elevated temperature is the cause of mass bleaching events, but it can be aggravated by changes in photosynthetically active radiation (PAR) or ultra-violet radiation (UVR) (Hoegh-Guldberg and Smith, 1989). Frequently corals recover from bleaching (Fitt et al., 1993; Lang et al., 1992; Mumby, 1999), but death may result if the stress is extreme or prolonged, as occurred in large areas of reefs in the Indian Ocean during 1998 (Sheppard, 1999; Wilkinson and Hodgson, 1999).

A bleaching response is also seen in other reef organisms living in association with symbiotic algae. Diverse groups from molluscs (e.g. tridacnid clams), sponges, foraminifers to other cnidarians (e.g. hydrocorals, zoanthids, sea anemones and alcyonarians) have all been observed to loose their algal symbionts during coral bleaching episodes (Glynn, 1993).

There has been a large increase in the number of reported mass bleaching incidents since 1979. This has been explained by the underlying trend of increasing sea temperature, upon which are superimposed periodic anomalies that exceed the threshold for coral thermal tolerance (Hoegh-Guldberg, 1999).

1.5.2.1. Differential susceptibility

Between species

Coral species differ in their susceptibility to bleaching (Williams and Bunkley-Williams, 1988); in general corals with the highest rates of skeletal growth and respiration are most susceptible to bleaching and associated mortality (Glynn, 1996). This has been attributed to increasing respiratory demands and diminished autotrophic capacity at higher temperatures (Jokiel and Coles, 1990). An alternative explanation is centred on the diversity of zooxanthellae within species; corals with multi-taxa communities of symbionts show increased resistance to bleaching than those hosting a single strain or species (McField, 1999; Rowan and Knowlton, 1995).

Within species

Some bleaching responses are notably patchy with bleached lone corals or groups of corals interspersed among normally coloured conspecifics (Jokiel and Coles, 1990; Williams and Bunkley-Williams, 1988). Some genetic individuals are more

susceptible to bleaching than others, and the observed patterns in bleaching may be related to the distributions of clonal colonies of these individuals (Edmunds, 1994). Bleached colonies of *Montastraea annularis* had a high probability (0.8) of having a nearest bleached neighbour of the same genetic individual, rather than a bleached colony of a different genet. Manipulative experiments with *Porites porites* also showed that clones belonging to certain genets were more susceptible to thermal bleaching than others (Edmunds, 1994).

Small-scale differences in susceptibility have been also related to depth; corals in shallow waters (1-5 m) often show higher rates of bleaching than deeper corals (Fisk and Done, 1985; Ghiold and Smith, 1990), though bleaching has been reported in deep waters too e.g. >60 m (Bunkley-Williams et al., 1991; Lang et al., 1988). This is usually attributed to higher ambient water temperatures and irradience levels. Lower incidences of bleaching may occur in shallow inshore lagoons with restricted water circulation compared with outer reef slopes (Sheppard, 1999; Sheppard et al., 2002), suggesting that corals living in habitats exposed to environmental extremes are more tolerant of warming events than those living in more physically constant environments.

1.5.2.2. Interaction of PAR and UVR

Frequently, warmer sea temperatures coincide with increases in solar radiation, particularly during very calm periods (Wilkinson and Hodgson, 1999). Furthermore, corals at the Society Islands (French Polynesia) and Mauritius (Indian Ocean) had unexpectedly milder responses (in terms of coral bleaching) to the warming event of 1998 than could be explained by temperature alone, that, in both cases, have been attributed to increased cloud cover during the critical period of elevated temperature (Mumby et al., 2001; Turner et al., 2000).

Commonly, the upper sides of colonies tend to bleach first and with the greatest intensity. Water temperature is unlikely to differ between the top and sides of a colony, and the most widely accepted explanation is that radiation (probably PAR but maybe also UVR) exacerbates the temperature response (Fisk and Done, 1985; Fitt and Warner, 1995; Harriott, 1985; Hoegh-Guldberg, 1999; Sheppard, 1999).

1.5.2.3. Physiological consequences of bleaching

Growth

Even where colonies survive, growth is compromised. *Montastraea annularis* colonies in Jamaica that bleached and subsequently recovered their pigmentation during the warming episode in 1987 had undetectable daily growth rates during the following five months, while growth in unbleached colonies was unaffected (Goreau and Macfarlane, 1990). This suggests that physiological disruptions associated with warming events have long-term consequences for calcification. Similar conclusions were reached in Florida (Leder et al., 1991), and the Ryukyu Islands, Japan (Suzuki et al., 2000). In contrast, a positive relationship has been found between temperature and calcification rate in massive *Porites* corals from the Great Barrier Reef, Australia, demonstrating that calcification rate has already increased over the last century in association with an increase in SST, and has the capacity to do so further in the immediate future (Lough and Barnes, 2000).

Other physiological effects include significant decreases in tissue biomass in corals bleached for long periods (> 1 year). This suggests that corals consume their own tissues in order to survive without zooxanthellae (Szmant and Gassman, 1990). Recent work has elucidated seasonal trends in tissue biomass (with lowest levels during warmest seasons) during non-warming years, which not only correlate with ambient temperature, but also with decreases in zooxanthellae parameters (density, chlorophyll *a* content) (Fitt et al., 2000). This has been interpreted as a normal, seasonal pattern driven by light and temperature acting on both algal and animal physiology, and has been termed physiological bleaching (*sensu* Fitt et al., 2001).

Decreased growth rates of bleached and recovered corals can decrease the capacity of corals to compete for space with other organisms, especially algae, that are not adversely affected by temperature increases (McCook et al., 2001).

Fecundity

Larval supply can also be reduced in the aftermath of warming events. During the reproductive season following warming in Florida, bleached *Montastraea annularis* colonies were incapable of gametogenesis, and may have reabsorbed early stage

oocytes, while recovered corals completed the energy intensive gametogenesis process (Szmant and Gassman, 1990). In Okinawa, following the 1998 warming event that devastated reefs, laboratory-based fertilization rates decreased from >94% to an average of 42% for five species of mass-spawning *Acropora* (Omori et al., 2001). In the Indian Ocean, coral recruitment appeared to almost completely miss a year (Sheppard et al., 2002). Thus there are serious implications regarding the supply of planktonic larvae following warming events.

Competitive ability

Diaz-Pulido and McCook (2002), tracked the fates of bleached corals over two and half years, quantifying the dynamics of algal overgrowth of affected colonies. Bleached but live corals were colonised by algal recruits, with higher overgrowth on more severely bleached colonies. No colonisation on healthy corals was recorded. Algal overgrowth in many cases led to partial mortality, though some corals were later able to recover.

Regenerative capacity

Bleached corals also have decreased rates of tissue and skeletal regeneration (Mascarelli and Bunkley-Williams, 1999), and during a warming event the ability of corals to maintain their colony integrity is impaired (Meesters and Bak, 1993).

Increased disease prevalence

Physiological stresses may compromise host resistance and increase frequency of opportunistic diseases (Harvell et al., 1999; Hayes and Goreau, 1998). The recent emergence of diseases and their rapid spread suggest that reef corals may be more physiologically stressed now than they have been in the past 5000 years (Aronson and Precht, 2001). Furthermore, coral diseases have been observed at high frequencies in the months following warming events (Kramer and Kramer, 2000), specifically infecting bleached corals (McField, 1999).

1.5.3. Recovery following bleaching incidents

Evidence of recovery from major natural disturbances such as hurricanes, volcanic activity and extreme low tidal exposure suggest that the rate of coral reef recovery is related to severity and scale of disturbance, but varies greatly from location to location (Glynn, 1993). Rapid recovery to pre-disturbance levels has been observed

in many areas where survivors nearby served as sources for recruitment (Colgan, 1987; Loya, 1976a; Pearson, 1981). Low rates of recovery can occur in coral communities that experience unusually frequent disturbances (Bunkley-Williams et al., 1991; Endean et al., 1988; Knowlton, 2001; Loya, 1976a; Pearson, 1981). Recovery also depends on the reproductive mode of surviving corals. The presence of brooding species can lead to rapid recruitment to disturbed areas (Hughes, 1985; Smith, 1992). Recovery may also occur rapidly via asexual fragmentation, but will be slow if recruitment is solely dependant on sexual reproduction from broadcast spawning species. This is the case in Western Atlantic reefs where recruitment rates of these corals are very low (Smith, 1992), and even slower if source populations are distant (Harrison and Wallace, 1990; Highsmith, 1982).

Recovery rates can be reduced when disturbances remove the largest corals in a population, either through death or partial mortality. Without the contribution of the largest corals, population fecundity is likely to decrease and other sources of mortality are likely to increase for surviving remnants.

Changes to the physical environment following warming events can also impede recovery. When the 1998 warming event killed the majority of corals (>90%) in the Chagos archipelago, bioerosion reduced dead coral skeletons to fields of rubble (Sheppard et al., 2002). Recruitment and survival of juveniles was assumed to be very low in such an unstable environment, due to the abrasion and souring action of mobile substratum. Furthermore, recruits that settled on dead coral skeletons remaining in growing positions will meet this problem at a later date when the skeletons are bioeroded and ultimately collapse. Also, algal pre-emption of space can reduce coral settlement and reestablishment (Connell et al., 1997; Goreau, 1992; Hughes, 1989; McClanahan et al., 2001b; Ostrander et al., 2000; Rogers, 1993; Shulman and Robertson, 1996).

1.5.4. Other implications of climate change

Impacts related to increasing temperature (above), are modelled in this study, as necessary data on which to base parameters is available. Climate change has other impacts, which are not modelled, but are noted below.

1.5.4.1. Carbon dioxide changes and ocean chemistry

Atmospheric carbon dioxide levels are predicted to increase in the future. Predictions are variable: current levels are around 360 parts per million (ppm) and will increase to between >450 ppm and >900 ppm by 2100 (IPCC, 2001). The important point here is that carbon dioxide enrichment of tropical coastal waters is predicted to decrease availability of bicarbonate ions for calcification by reef organisms, and hence will reduce growth. This is supported by decreased calcification rate in six out of seven studies carried out on different calcarious organisms (Gattuso et al., 1999). This response has been extrapolated to rates of CO_2 emissions from IS92 scenarios; the best case scenario (IS92c) causes a decrease in present day calcification of 10%, while the worst (IS92e) causes a decrease of 30%. These estimates, however, do not take into account possible compensatory acclimation mechanisms, or species variations.

1.5.4.2. Sea level rise

Sea level is predicted to rise between 1-10 mm $year^{-1}$, leading to increases of between 15 and 95 mm $year^{-1}$ by 2100 (IPCC, 2001). About half this increase is due to the thermal expansion of water with increasing temperature as a function of global warming, with most of the rest of the increase due to melting of mid and low latitude mountain glaciers (Pittock, 1999).

Some workers have suggested that this could be favourable for corals, as coral growth could keep pace with the flooding and reef flat dwelling species would benefit from vertical expansion (Smith and Buddemeier, 1992). However, reef growth is not the same as coral growth and whether reefs can keep up with rising sea level is questionable (Sheppard 2002b).

1.5.4.3. Increased storm frequency and intensity

High sea temperature is considered to enhance the genesis and sustained intensity of tropical storms (Pittock, 1999). While current ability to predict tropical storms is limited, there is general agreement that average intensity will increase by 10-20%, shifting overall intensities towards a greater frequency of extreme events.

1.5.5. Adaptation and acclimation

The question of whether corals have the capacity to adapt or acclimate to increased sea temperatures is central to the recovery and future survival of reefs. As yet there is no clear consensus, as results from laboratory studies are frequently in conflict with field observations. The arguments presented in this section are later used to develop model assumptions in Chapters 6 and 7.

Adaptation is the process of selection of individuals within a population that are most suited to cope with a changed environment. Acclimatization refers to the compensatory changes in metabolism or physiological responses of an organism exposed to variations in the environment. Mechanisms of acclimatization and adaptation operate over different temporal scales: acclimatization can occur very rapidly (e.g. production of heat shock proteins (hours)), while adaptation requires timescales of generations.

1.5.5.1. Adaptation

Corals have lived successfully in warmer and colder temperatures in the past. For example, around 2 million years ago massive coral extinctions at the start of the ice ages wiped out the most high temperature tolerant species, which were replaced by new low temperature tolerant species that are the ancestors of modern corals (Goreau et al., 2000). The present concern is that adaptations that would allow corals and their symbiotic algae to acquire high temperature tolerance that they now lack will take longer than that allowed by the present rate of warming.

Longevity of many corals means slow evolution of adaptive traits (Babcock, 1991). Asexual reproduction exacerbates this issue by further reducing potential for genetic recombination, thus populations may have low genetic diversity (though this is disputed, see review by Lasker and Coffroth, 1999).

In 1993, Buddemeier and Fautin (1993) put forward the adaptive bleaching hypothesis, suggesting that bleaching is an adaptive mechanism. This is based on observations that corals in habitats that are subjected to greater extremes tend to be less bleached than those in physically constant environments. Also, despite apparent

environmental adaptations, there are consistent taxonomic differences in vulnerability of corals to bleaching and mortality. Zooxanthellae have a rapid regeneration time compared to corals (days versus decades), indicating that alga may respond to local conditions quickly. Thus bleaching is seen as a high-risk opportunity for creating different host-symbiont combinations in response to a changing environment. This hypothesis has received much criticism though (e.g. Hoegh-Guldberg, 1999), not least because many bleached corals died in 1998. Also it is not known whether, after expelling one variety of zooxanthellae during thermal stress, corals do take up more heat tolerant strains, as many bleached corals retain substantial concentrations of their original zooxanthellae. This suggests that bleaching may have more to do with the expulsion of components of symbiosis damaged during heat stress than the total removal of one population of symbionts. There has been support for this hypothesis as more work has been done showing that corals can adjust their symbiont communities under stressful situations of high light (Baker, 2001), that zooxanthellae strains differ in their responses to elevated temperature, and bleached corals can take up zooxanthellae from surrounding water (Kinzie et al., 2001).

1.5.5.2. Acclimation

Photoacclimation, where modifications in behaviour, morphology, physiology and biochemistry allow corals to acclimatize to changes in solar radiation illustrates the capacity of corals to acclimate (see reviews by Barnes and Chalker, 1990; Brown, 1997). Gates and Edmunds (1999) suggested protein metabolism underlies acclimation responses in reef corals. Their conclusion is that corals with low growth rates and high metabolic rates, such as massive species, acclimatize more effectively than those with high growth rates and low metabolic rates, characteristically branching species. The complex symbiotic relationship between coral host and alga may also add a suite of acclimation mechanisms (Gates and Edmunds, 1999).

Interestingly, Meesters and Bak (1993) reported a community of acclimatized corals in the thermal effluent of a power plant. These corals were susceptible to bleaching during a warming event, but had higher temperature thresholds than corals upcurrent of the power plant. This acclimatized community had a different composition and lower diversity than the upcurrent community.

1.5.6. Predicted responses to climate change

1.5.6.1. Population responses

It is not clear how coral populations will respond to climate change. Modelled *Porites* spp. populations showed clear trends of decreased colony size and positivelys skewed size structures with increased frequencies of disturbance (Done, 1987; 1988). This response was consistent with or without exogenous recruitment. However, other workers have suggested the opposite to be likely, with recruitment processes interrupted and/or increased mortality in small sized colonies, resulting in coral populations skewed towards larger size classes (Bak and Meesters, 1999).

1.5.6.2. Community responses

Done (1999) suggested three adaptive modes for coral communities subject to climate change. If corals are able to adjust with environmental change, communities will be tolerant. Alternatively community structure may shift towards fast-growing ephemeral species, and even major phase shifts could occur as algae replace corals as the dominant benthic group. This thesis gathers available data, and, using the model described in the following chapter, provides predictions on reef communities under various scenarios.

1.6. Outline of chapters and aims

Arguments supporting the choice of model and processes included in it are addressed in Chapter 2. Aims of this chapter are to resolve methodological uncertainties and establish the necessary temporal and spatial framework for further model development. Some model properties are predetermined by the biology of the system, others require critical assessment of output to select optimal settings.

Chapter 3 explores the influences of the key parameter of disturbance, focussing on natural or 'background' disturbance. Two aspects are addressed: the proportion of the plot affected by disturbance and the sizes of disturbed patches. Specific objectives were to quantify influences of these disturbance parameters on the coral

community in terms of coral abundance patterns and diversity. Results are used to implement background disturbance within the model.

The sensitivity of the model to each of the coral life history processes is tested in Chapter 4. The aim is firstly to explore which parameters are important to model results. The ranges of conditions under which the model may be considered reliable are established. Two further areas are investigated here: interactive reach, and temporal variability in the supply of coral larval.

In Chapter 5, the model output is critically evaluated to assess its suitability, applicability and accuracy for predicting coral dynamics at community and population levels. Model predictions are assessed, not only in terms of coral cover and abundance, but also in terms of the much more informative coral population size structure. Simulations are run with increasing levels of background disturbance to assess the influence of this structuring force on modelled corals, and its interaction with individual life histories in generating community responses.

The impact of a single disturbance event on the modelled coral community is investigated in Chapter 6. The type of disturbance applied is a warming episode, causal agent of recent mass-mortality incidents. Probabilities of bleaching and mortality are assigned for corals using published reports. These are then applied to the modelled coral community, and impacts at varying intensities of warming are assessed. The aim here is to quantify the community response and subsequent recovery mechanisms, and the temporal scale over which they operate.

The overall objective of Chapter 7 is to employ the coral community model in conjunction with predictions of future warming episodes to gain insight into the resilience and vulnerability of coral communities to climate change over the course of the next 100 years. Here sea surface temperature predictions from a coupled ocean atmosphere general circulation model are applied, together with species-specific thermal responses for corals characterised in Chapter 6. Aims are to establish community responses and quantify changes in the size structure of coral populations with increasing frequency and intensity of warming events. The influence of environmental factors acting locally on corals that might operate synergistically with

warming events to intensify the rate and pattern of decline of coral communities are investigated in a suite of scenarios.

Chapter 2. Model structure

2.1. Objectives

The coral life history is a consequence of clonality. Because colonies are modular and have indeterminate growth, processes such as colony fission, shrinkage and fusion distort any simple relationship between size and age (Hughes and Jackson, 1980). Coral populations can be considered open, with sessile adult phases, but pelagic larvae that can disperse over great distance. Thus many standard/traditional demographic modelling techniques designed for individual organisms are not appropriate for open populations of sessile colonial invertebrates.

A spatially explicit model was used to examine the dynamics of coral communities. The spatial element is fundamental, primarily because rates of growth, recruitment and frequency of competitive interactions are dependant on the availability of space (Muko et al., 2001a; Roughgarden et al., 1985). These factors in turn influence the size structure of coral populations (Hughes, 1984), which can mediate other attributes such as fecundity (Soong, 1993) and mortality processes (Bak and Meesters, 1998; Hughes and Jackson, 1985). Also the spatial arrangement of coral species in relation to each other can be important in determining the outcome of competitive interactions and may play a role in structuring the community (Sheppard, 1982).

A key component in the model was a cellular automaton; these are temporally discrete, spatially explicit mathematical systems constructed of many identical components. Each component is simple and behaves according to preset rules, but the cooperative effect of many components acting together generates complex behaviour. Within this study, these components can be considered analogous to coral polyps, the fundamental modular units of coral communities. These are the foundation for the high level complexity of coral reefs, but are themselves simple, predictable and biologically well understood. Thus this model strives to generate

complexity from the base level upwards, using the known biology of the system components (coral polyps) to generate rules that govern their behaviour.

This chapter:

1. Defines which parameters of coral life history are to be included, and determines methods for implementing them within the model.

2. Tests structural properties of the model that are not predetermined by biology, to choose the most appropriate settings.

2.2. Methods

2.2.1. Assumptions

1. The model represents a spatially defined two-dimensional plot of reef substratum. Though a three dimensional model would add additional realism, all the modelled corals are zooxanthellate, thus require light for photosynthesis, so spatial patterns can be reduced to two-dimensional occupancy arrangements, without incurring enormous computational costs associated with an additional dimension.

2. The reef within the plot is homogeneous and uniformly suitable for coral recruitment and growth. Sand patches, for example, which are a component of real reefs, are excluded as this would reduce the amount of space occupied by corals and thereby reduce the quality of results.

3. The spatial resolution of the model is suggested by coral biology. Each cell in the array nominally represents 1 cm^2, a median sized polyp.

4. Coral growth is indeterminate (type II, *sensu* Sebens, 1987). This implies that there is no genetic constraint on maximum colony size, and colony size is a product of growth, competition, partial mortality and regeneration (Hughes and Jackson, 1985).

5. Growth can be limited by the availability of free space surrounding the colony (Hughes and Jackson, 1985).

6. Recruitment occurs once during each year. The majority (8/11) of Caribbean corals have one reproductive cycle per year, though some have more complex reproductive strategies (Szmant, 1986).

7. Recruitment originates from a regional pool of larvae, and is not dependant on the density of fecund corals in the plot. Coral larvae settle typically between 2-3 days from release for brooding species and 5-10 days from release for broadcast spawning species (Harrison and Wallace, 1990) and so would travel distances further than the spatial scale of the model during their pelagic phase.

8. Recruitment is space limited, and is proportional to both the abundance of larvae in the pelagic pool and the amount of unoccupied space within the plot (Roughgarden et al., 1985). Corals are planktivorus, so larvae can only settle on unoccupied space.

2.2.2. The model

The model represents a coral community within a two-dimensional plot located in a homogeneous reef habitat (Appendix 1). The plot is an array of cells, each of which can either be occupied by coral (or later by algae, Chapters 6 and 7) or is vacant (bare substratum). The automaton, depending on the current occupancy of a cell, and those adjacent to it, generates changes in the array, according to simple preset rules dictated by coral biology. This neighbourhood may be four cells (Figure 2.1) in its simplest form (Von Neuman neighbourhood) or can be changed to larger sizes, as during some simulations in this section.

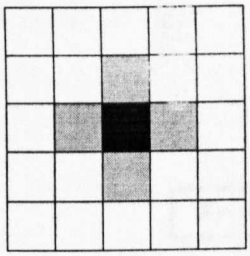


Figure 2.1. Von Neuman neighbourhood. Black indicates the focal cell, and grey indicates its neighbourhood.

Each cell in the array nominally represented 1 cm^2, as noted earlier. Other model properties including the size of the plot, structure of the plot edges, and temporal scale were tested to determine optimal levels.

2.2.3. Simulation of life history processes

The cellular automaton sits within a larger model consisting of several modules. Each life history process was implemented by a separate module, and these modules were linked together into a loop representing one year cycle, termed years from this point forward (Figure 2.2). The cellular automaton handled growth and aggression processes. This formed the core of the model, and other processes such as recruitment and mortality impacted upon it. This part of the model could be iterated more than once each year cycle, and was tested for the optimal time increment later in this section.

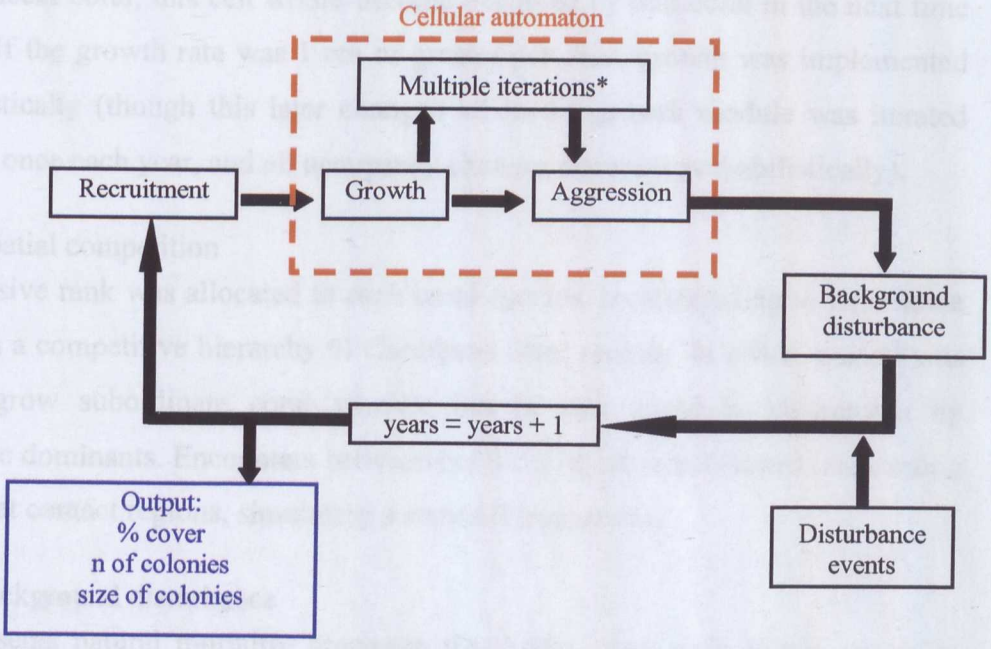


Figure 2.2 Schematic diagram of model structure representing one year. A series of connected modules handled life history processes. * The cellular automaton core could be iterated more than once each year (see Section 2.2.6).

2.2.3.1. Recruitment

Recruitment was implemented once each year, and coral species were assigned densities at which they recruited into the plot. At the start of each simulation, Poisson probability distributions were constructed, assigning a probability to numbers of recruits for each mean rate of recruitment. A pseudorandom probability was generated, and this determined the number of potential recruits in the pool for that species during that year. For each recruit, further pseudorandom number generation was used to specify coordinates within the array for attempted settlement, and if this cell was unoccupied, recruitment was successful. The species order of recruitment was randomly allocated each year, as this was perceived as a potential source of bias as it can be in plants (Ross and Harper, 1972).

2.2.3.2. Growth

Coral growth was implemented in two dimensions as a radial expansion. Each coral species was allocated a growth rate. Each cell in the array was systematically examined to determine occupancy in the next time iteration. Occupancy changes came about when a cell adjacent to a colony was vacant (or occupied by a subordinate species, see below). In cases where the growth rate of the species was <1

cm, a pseudorandom number was generated and if less than the probability of growth of the adjacent coral, this cell would become occupied by that coral in the next time iteration. If the growth rate was 1 cm or greater per year, growth was implemented deterministically (though this later changed when the growth module was iterated more than once each year, and all occupancy changes occurred probabilistically).

2.2.3.3. Spatial competition

An aggressive rank was allocated to each coral species, corresponding to its relative position in a competitive hierarchy of Caribbean coral species. In effect, a coral was able overgrow subordinate coral species, but in turn could be overgrown by competitive dominants. Encounters between corals of equal rank resulted in cessation of growth at contact regions, simulating a standoff interaction.

2.2.3.4. Background disturbance

This represents natural mortality processes that bring about total colony mortality (death) or partial mortality (shrinkage) of coral colonies. Patches were disturbed each year. In an 'unimpacted' system (not subjected to large scale disturbance events), aside from overgrowth during competition, background mortality was the only way that coral was removed from the system. Details of the selection, size and number of patches disturbed are given in the following chapter, but essentially, array coordinates were specified using pseudorandom number generation, and became the centre of circular areas that were reset to bare substratum. Later, additional mortality arising from impacts are implemented together with this background mortality.

2.2.3.5. Model output

Firstly, output from the model was taken at the end of each year as simple percent cover by coral species. In addition, a connected component analysis was developed to calculate colony sizes. This enabled population size structure assessment, a much more informative data type than relative cover (Bak and Meesters, 1998). Basic rules provided the framework of this analysis. Adjacent cells from the same original (genetic) coral recruit would be considered part of the same colony. Array cells in diagonal arrangement would also be counted as parts of the same colony, but any further spatial separation would be regarded as two colonies. Thus, the model could account for complex processes resulting from clonal life histories such as colony

fission and fusion. Later chapters depend heavily on the ability to implement this technique, which is considered a significant improvement to simple cover estimation.

2.2.4. Structure of plot edges

While some properties of the model were predetermined by the ecology of the reef system (e.g. the spatial nature of the model, and the spatial equivalence), others were not. These needed to be tested systematically, in order for the model output to be at an informative resolution, and for computational efficiency. Model starting conditions were standardized; simulations were consistently initiated from bare substratum.

As the plot size was finite, plot edges must be accounted for. Two main treatments of edges of spatial models exist: 1) island edge structure (or zero flux boundary conditions), where complete isolation in a vacuum is assumed and no organisms or energy can flow across the boundaries, and 2) toroidal edge structure (or periodic boundary conditions), where the edges join left edge to right and top to bottom to form a two-dimensional torus with continuous space (Inghe, 1989). The effectiveness of these two methods was compared. It was hypothesised that island edge structure would create refuges for competitively subordinate coral species, as competition would be from one direction.

Life history attributes for five hypothetical species were used, (Table 2.1), though rates of recruitment were reduced to 1 recruit 9 m^2 yr^{-1} to prevent fecund species from swamping available space as bare substratum was required to examine space occupancy. Ten replicates of each edge structure were run to estimate variability generated by stochastic processes in the model. Output, as proportion of coral to bare substratum was collected after 10 years. Increasingly large bands round the edge of the plot comprising of increasing percentages of the total plot area were presumed to be the "edge"

Table 2.1 Life history attributes for five hypothetical coral species used for testing of structural properties of the model.

Species	Competitive rank*	Growth rate	Recruitment rate
1	1	2	45
2	2	3	18
3	3	2	5
4	4	1	1
5	5	1	1

* The most aggressive coral is ranked 5 and the least, 1.

2.2.5. Size of plot

Different sized plots were tested to determine 1) whether plot size has an effect on model output and 2) the smallest sized plot to yield repeatable results. It was hypothesised that plot size would correlate negatively with variability between replicates. This was tested using a range of different sized plots, representing 1 m^2 (i.e. 100 x 100 array), 4 m^2, 9 m^2, 16 m^2 and 25 m^2. Apart from plot size, the experimental design was as shown in Table 2.2, and species attributes were as Table 2.1, although recruitment values varied with plot size (Table 2.3).

Table 2.2 Experimental design

Attribute	Setting
Starting condition	Bare substratum
Plot size	9 m^2
Plot edges	Toroidal wrapping
Number of replicates	10
Run duration	25 years

Table 2.3 Recruitment values of five hypothetical species used in simulations testing the effect of plot size. The ratio of recruits by species was kept consistent across different sized plots.

Species	1 m^2 yr^{-1}	4 m^2 yr^{-1}	9 m^2 yr^{-1}	16 m^2 yr^{-1}	25 m^2 yr^{-1}
1	5	20	45	80	125
2	3	12	27	48	75
3	2	8	18	32	50
4	1	2	9	16	25
5	1	2	9	16	25

Model output as relative species cover was taken after 25 years, and from this the coefficient of variation was calculated for each species (mean/SD), and expressed as a percentage.

2.2.6. Time increment

Simulations with increasing numbers of growth iterations per year were carried out in order to determine the most appropriate time scale increment for the model to capture events of interest. During each model year, growth was called either once, four times or twelve times, and the growth rate of each species divided by this factor. The design of the experiment was identical to previous ones (Table 2.1, Table 2.2).

After results were compared, a further analysis was undertaken to determine the effect of the increased number of growth iterations per year on modelled coral cover. A simple program was written to simulate early colony growth, where a colony initially occupied one cell and was allowed to grow over the course of one year. The number of additional cells it occupied at the end of the year was recorded. Each set of parameters was replicated 100 times. From this, correction factors were derived for each growth rate and time scale, to remove the bias from multiple growth iterations per year. Finally the model was run again with the correction factors to confirm that there were no differences in net abundance attributable to the number of growth iterations each year.

2.2.7. Module order

It was thought possible that the order in which modules that handle each life history process are called in the model could potentially have an influence on model output. To test for this, a series of simulations were run with modules implemented in reverse order. Results were compared to simulations with the original sequence (Figure 2.2). The design of the experiment was as before (Table 2.1, Table 2.2).

2.3. Results

2.3.1. Structure of plot edges

Plot edges had lower coral cover than central areas when island edge structure was used but not when using a torus system (Figure 2.3). This difference was manifest through a large proportion of the plot (i.e. even when the outer 50% of the plot was considered to be the edge, some differences were still detected). This was due to coral colonies that overlapped edges being effectively lost from the system using an

island structured plot. By contrast, coral cover was constant throughout the plot within a toroidal structured plot, though variability within replicates increased as sample size (amount of plot considered edge) decreased. Therefore toroidal edge structure was adopted.

2.3.2. Size of plot

Variance within replicates using the hypothetical species decreased with increasing plot size (Figure 2.4). While the three largest plot sizes had consistent levels, variance increased markedly for plot sizes below 9 m^2, indicating a potential lack of repeatability in model output, or a requirement for large numbers of replicates. Variance in abundance also appeared to be related to life history; species 1 had >3-fold variance of other species, and this was consistent across all plot sizes tested.

2.3.3. Time increment

Time increment, (number of growth iterations per year), had a strong influence on the modelled coral community (Figure 2.5). Corals grew faster under conditions of multiple growth iterations per year, leading to increased rates of species succession. For example, species 1 reached maximum abundance at 7 years with 1 growth iteration $year^{-1}$, 6 years with 4 growth iterations $year^{-1}$ and 5 years with 12 growth iterations $year^{-1}$.

Differences in abundance between time increments were statistically significant (Table 2.4). The interaction term was also significant, indicating that the number of growth iterations $year^{-1}$ had more influence on some species than others.

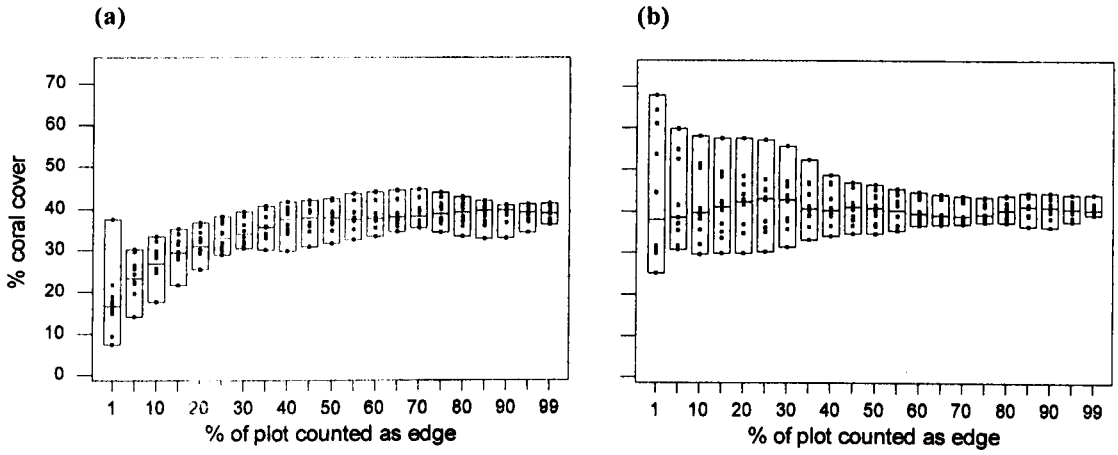


Figure 2.3 Effect of edge structure on model output. (a) island edge structure and (b) toroidal edge structure. Total coral cover (%) against an increasing edge proportion of the plot at 10 years. Data range with median and individual data points shown.

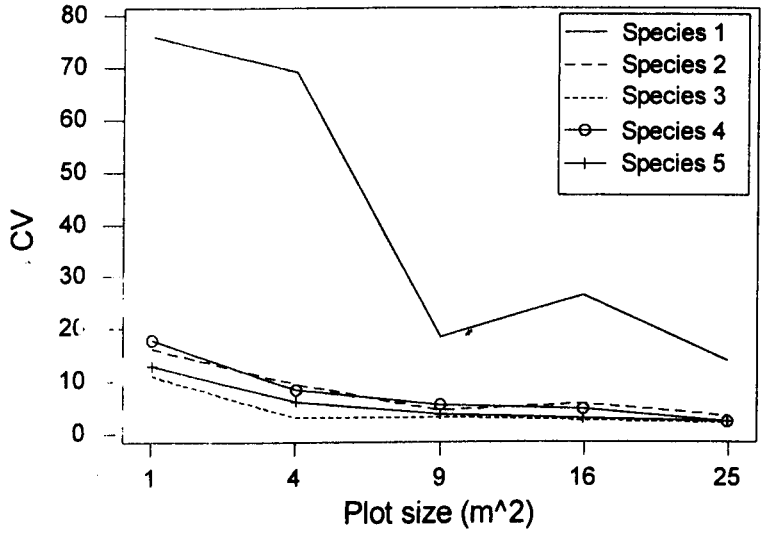


Figure 2.4 Effect of size of modelled plot on replicate variability. Coefficient of variation (CV) for hypothetical species 1 to 5 for plot sizes representing 1 to 25 m^2, n = 10 replicates. Output taken as percent cover at 25 years.

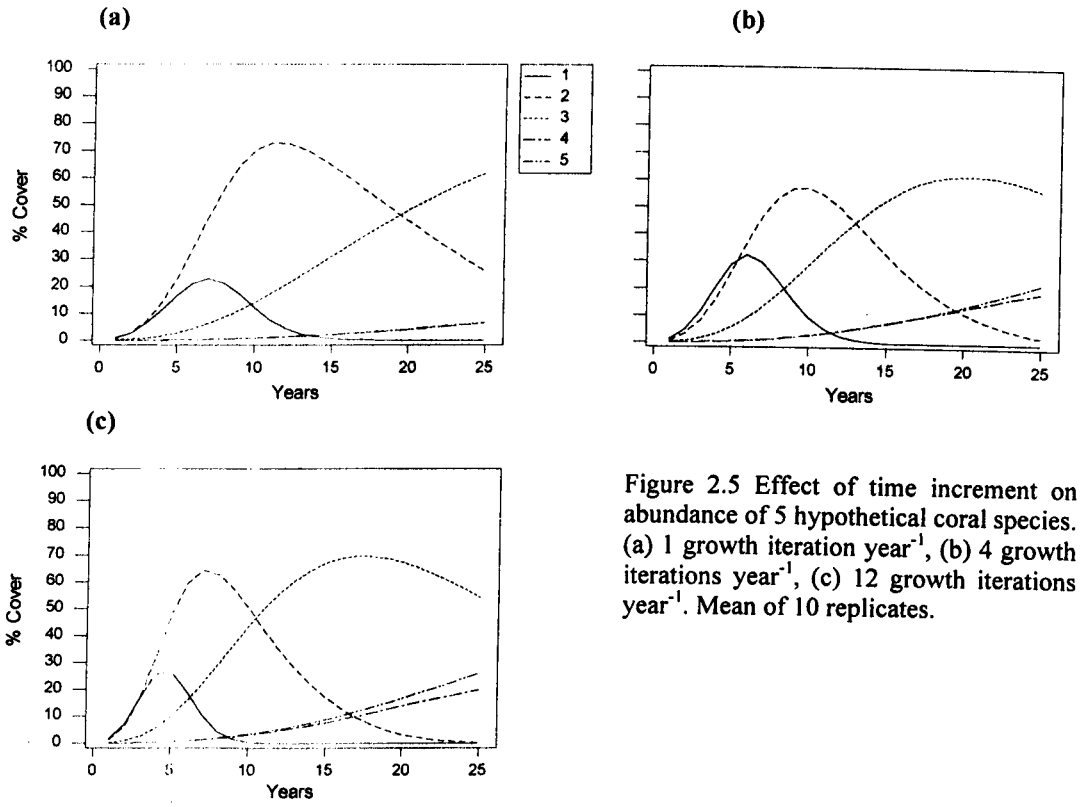


Figure 2.5 Effect of time increment on abundance of 5 hypothetical coral species. (a) 1 growth iteration year^{-1}, (b) 4 growth iterations year^{-1}, (c) 12 growth iterations year^{-1}. Mean of 10 replicates.

Table 2.4 Two-way ANOVA (species x time scale) carried out on log-transformed abundance data at 25 years for the 3 most abundant species. Time scales tested were 1, 4 and 12 growth iterations year^{-1}, n = 10.

Source	DF	SS	MS	F	P
Species	2	7.4	3.72	762.43	<0.001
Growth rate	2	2.25	1.12	230.86	<0.001
Interaction	4	1.5	0.37	77.68	<0.001
Error	81	0.39	0.005		
Total	89	11.62			

This difference in net growth rate with increasing number of growth iterations per year was explored. Early colony growth was simulated over the course of one year (see Methods, Section 2.2.6). The relationship between time increment and net colony growth was again clearly influenced by species growth rate (Figure 2.6). With high numbers of growth iterations per year, a colony expands to colonise adjacent cells in the array, and these cells could themselves grow in later growth iterations, raising the overall growth rate away from preset values. In order to remove this bias, correction factors were calculated for each growth rate at each time increment, by repeating the early growth simulations with decreased probabilities of growth, until similar net colony growth rates were obtained as those from a time scale of 1 growth iteration year^{-1} (Figure 2.7).

The model was run again with the derived growth factors to confirm that net growth rates were corrected by this technique to preset levels. There were no significant differences in abundance attributable to time scales between 1 and 4 growth iterations year^{-1} (though data from 12 growth iterations year^{-1} was not included in this analysis due to increased variance) (Table 2.5). Therefore four growth iterations per year were selected as most suitable.

Table 2.5 Two-way ANOVA (species x time scale) carried out on log-transformed abundance data at 25 years for the three most abundant species. Time scales tested were 1 growth iteration year^{-1} and 4 growth iterations year^{-1}, run with correction factors, n = 10 replicates.

Source	DF	SS	MS	F	P
Species	2	8.64	4.32	901.57	<0.001
Growth rate	1	0.14	0.014	2.99	0.09
Interaction	2	0.003	0.0014	0.28	0.75
Error	54	0.26	0.005		
Total	59	8.92			

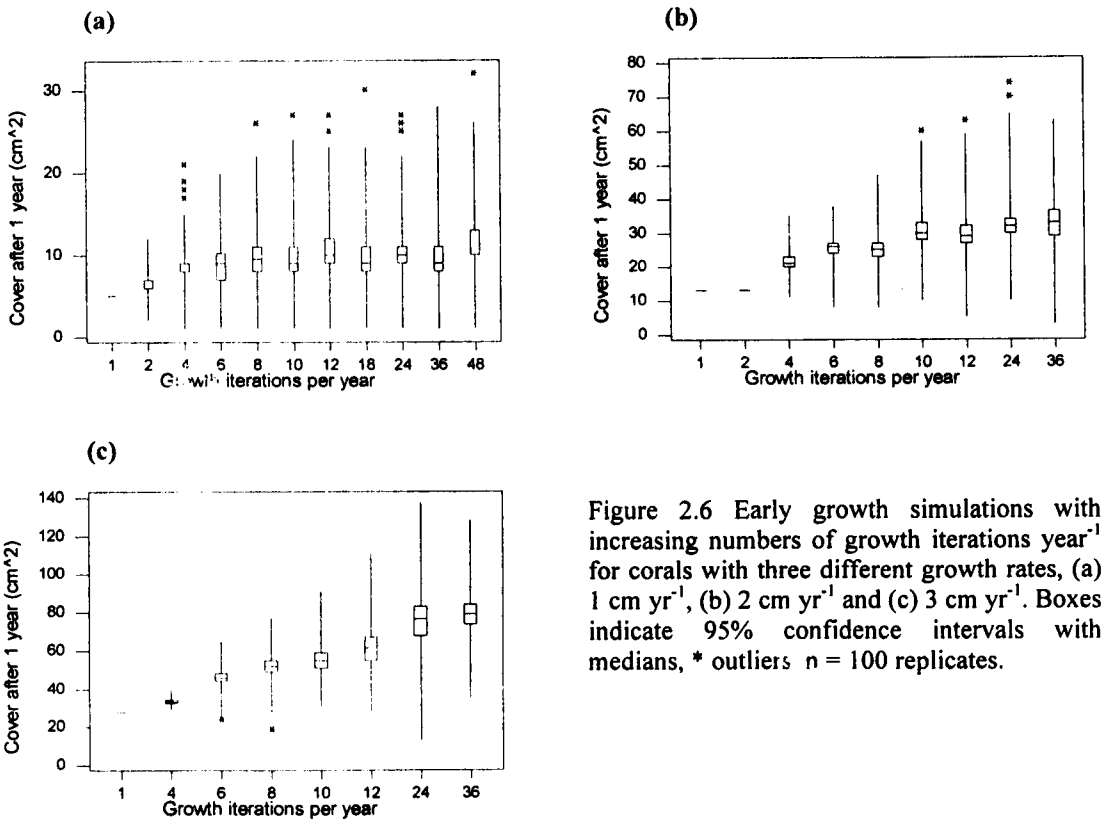


Figure 2.6 Early growth simulations with increasing numbers of growth iterations year^{-1} for corals with three different growth rates, (a) 1 cm yr^{-1}, (b) 2 cm yr^{-1} and (c) 3 cm yr^{-1}. Boxes indicate 95% confidence intervals with medians, * outliers n = 100 replicates.

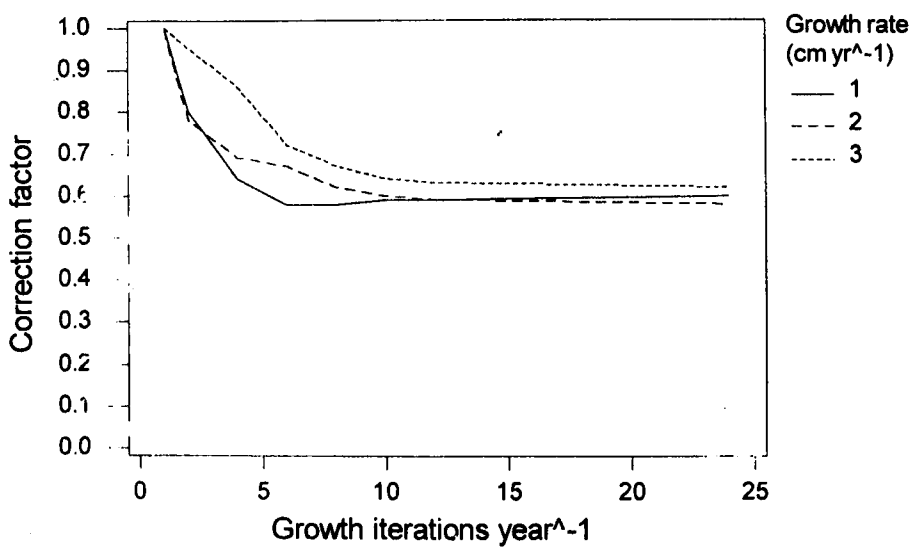


Figure 2.7 Derived correction factors plotted against time increment (number of growth iterations year^{-1}) for three growth rates.

2.3.4. Module order

The sequence of implementation of modelled life history processes did not affect the abundances of five species (Figure 2.8). No differences in percent cover could be detected between orderings (Table 2.6).

Table 2.6 Two-way ANOVA (species x sequence of modules) carried out on abundance data at 25 years for the four most abundant species, n = 10.

Source	DF	SS	MS	F	P
Species	3	52574.2	17524.7	2989.66	<0.001
Sequence	1	0	0	0	>0.999
Interaction	3	45.7	15.2	2.6	0.059
Error	72	422	5.9		
Total	79	53041.9			

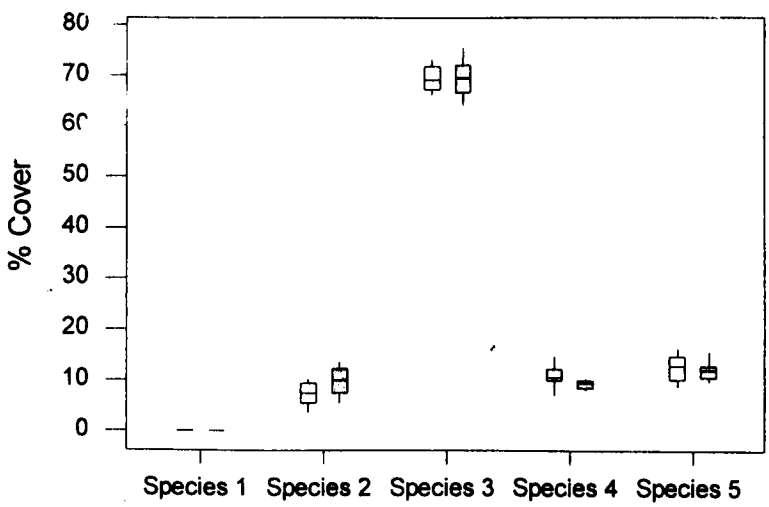


Figure 2.8 Effect of module order on abundance of 5 hypothetical species at 25 years. Unfilled boxes indicate simulations with normal ordering, filled boxes reverse ordering, boxes indicate 95% confidence intervals, n = 10.

2.4. Discussion

Testing these structural properties clearly determined which settings were most suitable for robust and repeatable results. All the variations in structural properties led to changes in model output, which allowed selection of the optimum value, with the exception of the sequential ordering of modules handling life history processes.

Toroidal edge structure mitigated edge effects, and so was adopted. The alternative technique of removing a band from the edge of the plot prior to analysis is not a viable option given that edge effects were demonstrated through >50% of the plot. The structure of plot edges is rarely specified for published spatial models (Table 2.7), but this study indicates that this is essential and that model output data are likely to be compromised without consideration of this.

Optimum plot size is 9 m^2, which was therefore adopted. This is the smallest size to generate results without excessive variability between replicates. The selected array size of 300 x 300 cells is substantially larger than many previous models, the most directly comparable being those by Crimp and Braddock (1993), Reichelt et al. (1985) and Maguire and Porter (1977), which simulate coral communities at a local scale (metres) (Table 2.7). This highlights the comparatively high spatial resolution of the current model, which, as noted, was preferred also on the basis of coral biology. The advantages of modelling corals at this high spatial resolution are two-fold: 1) highly informative output can be generated, namely the size structure of coral colonies (Bak and Meesters, 1998) (see later chapters), while other models have been restricted to simplistic measures of abundance or cover (Table 2.7). 2) vacant space is better accounted for. Models with low spatial resolution falsely allocate relatively large areas (e.g. up to 400 cm^2) to small and slow growing corals, concealing that some space, in reality, may be available to other corals. The ability to model corals at high spatial resolutions reflects advancements in computers over the last decade.

The time step chosen for this model was four growth iterations per year. The reason for this was to consistently implement probabilistic growth. If growth were iterated

only once each year, some species would be implemented deterministically (those with growth rates of 1 cm radial increase and above), while others would be implemented probabilistically. Iterating growth four times each year had the added advantage of decreasing model runtime, as the neighbourhood was reduced to the adjacent four cells, whereas with deterministic growth implementation, the neighbourhood was dictated by the greatest rate of growth, i.e. 3 cm. In future, variable growth with seasons may be implemented. There is evidence to suggest that calcification occurs more rapidly during winter than summer months (Carricart-Ganivet et al., 2000), but since the majority of measurements are published as radial increases $year^{-1}$ (Huston, 1985), it is currently not possible to simulate effects of seasonality. Other life history processes were implemented once each year; this is intuitive given the temporal scale of events (e.g. recruitment, see Assumptions). Previous models have consistently use time steps of 1 year for similar reasons to those outlined above (Crimp and Braddock, 1993; Inghe, 1989; Maguire and Porter, 1977).

Two other spatially explicit modelling techniques could have been applied to coral communities. 1) Reaction-diffusion (RD) models have continuous space and are modelled by partial differential equations (in ecological terms, the reaction is the local population dynamic and the diffusion is the regional or global dispersal of populations). The main drawback of this technique is the treatment of organisms as densities, which, in the case of corals, means the loss of valuable demographic information and local stochasticity. Though an interesting solution to this was presented by Muko et al. (2001b), who included size structuring within local populations, this was restricted to a single species community. 2) Coupled map lattices, like cellular automata, divide space into discrete compartments, but states within these compartments are continuous, and dispersal between compartments occurs via simple diffusion equations or density dependant dispersal. While they are generally applicable to sessile communities (Karlson and Buss, 1984; Karlson and Jackson, 1981), disadvantages the same as those for RD models.

Table 2.7 Structural properties of some previous spatial models of sessile communities from marine and terrestrial systems.

	(Inghe, 1989)	(Maguire and Porter, 1977)	(Reichelt et al., 1985)	(Crimp and Braddock, 1993)	(Karlson and Buss, 1984; Karlson and Jackson, 1981)	(Burrows and Hawkins, 1998)	(Johnson and Preece, 1992; Preece and Johnson, 1993)	This model
Array size	60 x 60	25 x 25 to 500 x 500	120 x 60	100 x 100	40 x 40	25 x 25	33 x 120	300 x 300
Area simulated	1.2 x 1.2 m	5 x 5 m	12 x 6 m	5 x 5 m	?	25 x 25 m	165 x 600 km	3 x 3 m^2
Spatial resolution (size of cells)	2 cm	1, 2, 5, 10 and 20 cm	10 cm	5 cm and 10 cm	?	1 m	5 km	1 cm
Time step (years iterations^{-1})	1 generation (= 1 year)	1 year	?	1 year	?	?	?	4 x year and 1 x year[1]
Temporal scale (iterations run^{-1})	250	20	240	500	25	230	?	100-500
Taxonomic resolution	Species	Species	Functional groups	Functional groups	?	Community states	Coral cover states	Predominately species[2]
N groups	2	6	5	5	10	5	5	10
Output	N ramets	% Cover	% Cover	% Cover	% Cover		Mean state	% cover, CSS[3]
Edge structure	Toroidal	?	?	Island	?	Toroidal	?	Toroidal
Neighbourhood	12	?	4	?	?	?	8	4
System modelled	Herbaceous perennial plants	Eastern Pacific coral community	Coral reef community (3 corals, soft coral and algae)	Great Barrier Reef coral community (all groups represent corals)	Sessile benthic community (non-scleractinian)	Temperate rocky shore community	Great Barrier Reef coral communities (v. low resolution)	Caribbean coral community

[1]Growth was iterated 4 times each year, recruitment and mortality were iterated once each year
[2] Some species complexes
[3] CSS – colony size structure

Chapter 3. Background disturbance

3.1. Objectives

Background disturbance is an important process structuring coral communities (Connell, 1978; Connell et al., 1997). Within the scope of this model, background disturbance refers to natural abiotic and biotic processes that generate coral mortality. Comparatively little is known about natural rates of disturbance; the literature is dominated by reports documenting impacts of rare catastrophic events (Bythell et al., 1993a; Ostrander et al., 2000; Rogers, 1993; Witman, 1992; Woodley et al., 1981), or anthropogenic disturbances (see review by Dubinsky and Stambler 1996). This is probably because background disturbance is difficult to measure due to the wide-ranging spatial and temporal scales over which it operates, and because visible effects of disturbance manifest as coral mortality are variable and transient (e.g. coral species regenerate lost tissue at different rates, Bak, 1983; Meesters et al., 1997).

It is clear that disturbance affects corals according to their colony size; small corals are more vulnerable to whole colony death than large ones that, in turn, are vulnerable to partial mortality (Bak and Meesters, 1998; Gosselin and Qian, 1997; Hughes, 1984; Hughes and Jackson, 1985). Some species are more susceptible than others, due to a combination of morphological (e.g. fragile colony structure) and physiological characteristics (e.g. regeneration capacity) (Bak and Luckhurst, 1980; Hughes and Jackson, 1985; Meesters et al., 1997). This is reflected by the marked contrast in composition between juvenile and adult coral populations (Bak and Engel, 1979; Rylaarsdam, 1983). This implies that, together with the supply of recruits, post-settlement mortality processes are important in shaping the adult coral community.

There are two obvious approaches to simulating background disturbance processes: 1) to divide coral populations into size classes and assign rates for total colony mortality and partial mortality (Crimp and Braddock, 1993; Done, 1987), or 2) to simulate disturbance over spatial and temporal scales as discrete patches impacting

one or more coral colonies. The second approach was taken for two reasons: 1) an enormous amount of information is required for the first approach, taking long periods to collect (decades), and is currently not available for more than a couple of species (Hughes and Jackson, 1985), and 2) exploring patch dynamics generates a better understanding of the spatial nature of disturbance, and yields results on continuous scale of colony sizes enabling detailed demographic analysis.

In this chapter the influences of two key parameters of disturbance are explored: 1) the proportion of the plot affected by disturbance and 2) the sizes of disturbed patches. Specific objectives were to quantify their influence on the coral community in terms of coral abundance patterns and diversity. Results were used to develop the mechanism for background disturbance implementation within the model.

3.2. Methods

3.2.1. Assumptions

1. Mortality occurs as either total colony mortality (death) or partial mortality (shrinkage). Rates for each type of mortality are related to colony size (Bak and Meesters, 1998; Gosselin and Qian, 1997; Hughes, 1984; Hughes and Jackson, 1985).

2. Bare patches on a reef occur at different scales of time and space, ranging from frequent small openings to rare events where large areas are cleared (Connell and Keough, 1985).

3. Mortality rates vary with species. Out of the coral groups modelled, *Agaricia* spp. has the highest rate of tissue turnover (Bak and Luckhurst, 1980; Hughes and Jackson, 1985; Meesters et al., 1997). Others were assigned as below.

3.2.2. Species attributes

Life history attributes were assigned to ten coral species after reviewing the literature. Some species were grouped, as observations from older literature do not

account for recent taxonomic advances, for example *Montastraea annularis* refers to the species complex, and includes *M. annularis, M. faveolata* and *M. franksi* (Weil and Knowlton, 1994), *Madracis* spp. includes *M. pharensis, M. formosa* and *M. decactis* (Diekmann et al., 2001), and *Agaricia* spp. includes non-plating growth forms such as *A. agaricites, A. humilis* and *A. tenuifolia*. Each species or group of species was assigned a rate of recruitment, growth and a competitive rank (Table 3.1).

1. Rates of growth were restricted to measurement from corals growing between 10-20 m depth, as coral growth rate varies with depth (Huston, 1985). These measurements were based on radial skeletal extension rates from sections through coral skeletons (see Appendix 2.1).

2. Aggressive ranks were assigned from field observations made on transects done in Utila, Honduras in August 1999, in which all interactions encountered between hard corals were investigated. Adjacent colonies were considered to be interacting if the inter-colony distance was between 1-5 cm (*sensu* Lang and Chornesky, 1990). Outcomes of interactions were determined by the presence of necrotic tissue, excessive mucus or exposed skeleton along the region of contact between the species, (after Lang, 1981, Sebens, 1976), and the direction of overgrowth if present. Using this information, a hierarchy of competitive ability was constructed for the 10 coral species in the model (see Appendix 2.3). While it is known that outcomes of aggressive interactions may be variable between two corals (Bak et al., 1982, C. Johnson, pers. comm.), in an effort to keep the model simple, interactions between a pair of corals were only allowed one outcome; the outcome most frequently encountered in field observations.

3. Rates of recruitment were based on settlement experiments where tiles or other substrata were placed on the reef and the number of juvenile coral colonies counted after a period of time. Varying experimental protocol were used to gather these data, so published reports are not directly comparable. However, clear trends can be seen in the proportion of recruits by species, so based on this rates of recruitment were assigned (see Appendix 2.2).

Table 3.1 Parameter values assigned for life history processes for the ten modelled corals.

Coral group	Code	Aggressive rank	Growth rate	Recruitment rate
Montastraea cavernosa	1	10	0.5	1
Stephanocoenia michelinii	2	4	1	7.2
Agaricia spp.	3	4	2	469.6
Eusmilia fastigiata	4	6	1	1.2
Meandrina meandrites	5	8	2	1.2
Montastraea annularis	6	9	1	15.6
Colpophyllia natans	7	5	1	1.7
Porites astreoides	8	4	0.5	71.1
Madracis spp.	9	3	2	25
Siderastrea siderea	10	4	0.8	8.5

3.2.3. Proportion of the plot disturbed

In order to quantify the influence of increasing disturbance, simulations were run with varying proportions of the plot disturbed. The size of disturbed patches was kept constant at 5 cm radii. Disturbance was implemented by initially calculating the number of disturbed patches required to disturb a total proportion of the plot to preset levels (0, 0.1, 0.2, 0.4 and 0.6). Disturbed patches were created using pseudorandom number generation to assign coordinates for the centre of each disturbed patch and array cells within a 5 cm radius of the patch centre were 'disturbed' or reset to bare substratum.

Ten replicates were made for each disturbance setting, and the starting conditions in each case were bare substratum. Each simulation was run for 500 years and output was taken throughout the simulation as percent cover by coral species. The number and size of colonies were collected at the end of the simulation.

To assess how mortality is distributed amongst different sized colonies, and the nature of this mortality (i.e. total colony mortality or partial mortality), coral populations were examined at 500 years, before and after the disturbance routine. The number of colonies by species and by size class on a log scale[6] affected by 1) total colony mortality and 2) partial mortality was recorded. A mortality index was

[6] A log scale was used because coral populations are heavily skewed with small colonies over-represented, and a transformation to a log scale normalises most populations and enables further analysis (Bak and Meesters, 1998).

constructed to yield a value describing the relative importance of each mortality type (Equation 3.1)

$$M_{s,c} = \log_{10}\left[\frac{T_{s,c}}{P_{s,c}}\right]$$

Equation 3.1 Index of mortality. $M_{s,c}$ indicates the mortality ratio of coral species s, colony size class c, $T_{s,c}$ indicates number of colonies which underwent total mortality (from species s, and size class c), while $P_{s,c}$ indicates the number of colonies that underwent partial colony mortality (for the same species and size class), both at 500 years.

This mortality index was calculated for four coral species that were sufficiently abundant at each disturbance level to enable comparison. The modal size class for each species at each disturbance level was obtained from log transformed size frequency distributions. In rare cases where the size structure showed bimodality (with a large amount of colonies in the smallest size class in all such cases), the larger size class was taken as the mode.

Finally, diversity was calculated from percent cover at 500 years using a diversity index (Shannon and Weaver, 1948), (Equation 3.2).

$$H' = -\sum p_i (\ln p_i)$$

Equation 3.2. Diversity index (Shannon and Weaver, 1948), where p_i indicates the proportion of the total count of the ith species.

3.2.4. Effect of disturbed patch size

The influence of disturbed patch size was assessed, in this case total quantity of disturbance was kept constant by maintaining the proportion of the plot affected at 0.2, while disturbed patches were varied in size, with radii of 1 cm, 3 cm, 5 cm, 10 cm and 20 cm. As with the previous study, the number of patches required to make up the total area disturbed was calculated at the start of each simulation, and disturbance was implemented in the same way. Each scenario was replicated ten times and the model was run for 500 years. The relative importance of mortality processes on population size structure (Equation 3.1) and community diversity (Equation 3.2) was assessed as before.

3.2.4.1. Using a powerlaw function to assign disturbed patch size

Having established that the size of disturbed patches strongly influences the structure of the modelled community and forces population structure of species within it, a powerlaw model was introduced to the coral community model to distribute disturbed space into patches. This was based on the assumption that open patches on a coral reef are created at different scales in time and space (Section 3.2.1). This provided a way of allocating patch sizes by assigning probabilities to achieving a disturbed patch of a certain radius (Equation 3.3).

$$r = R0P^{(-1/a)}$$

Equation 3.3 Powerlaw function. R0 is the radius of the smallest patch (1 cm, as dictated by the spatial resolution of the model), a is a constant controlling the shape of the curve (this was tested later in this section), and P is a probability.

The module implementing this function firstly calculated the radius of patches from P = 0.001 to P = 1, iterated in steps of 0.001, and calculated mean patch size (as a radius). The mean patch size was then used to determine the number of disturbed patches for preset amounts of disturbance (i.e. a proportion of 0.15 of the total plot area). During simulations, within the disturbance routine, the preset number of disturbed patches was then created, using pseudorandom numbers to obtain P, and thus a radius would be assigned for each patch (which would then be positioned pseudorandomly as before).

However, the constant a required testing to find its optimal value. This determines the shape of the curve or steepness, which in turn controls the distribution of patch sizes. This was carried out by testing the influence of a range of different values for a. (1.25, 1.5, 1.75 and 2). The lowest value generated the largest mean patch size, while the largest value generated the smallest (Figure 3.1, Table 3.2), hence more patches were required to makeup the total area disturbed to the preset level of 0.15 of the plot area when using a at 2 than at 1.25.

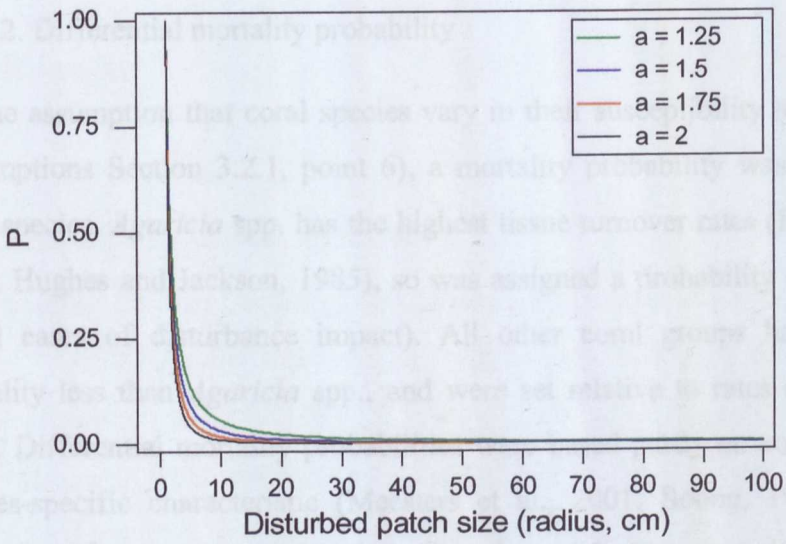


Figure 3.1 Influence of *a* on the shape of the powerlaw model.

Table 3.2 Size of disturbed patches with different values for *a* (constant in powerlaw function used to assign probabilities for radii of disturbed patches)

a	Average patch radius (cm)	Number of patches year^{-1}	Total area disturbed year^{-1} (cm^2)
1.25	437.76	30	13132.8
1.5	98.36	138	13573.13
1.75	37.54	359	13476.86
2.0	20.41	663	13533.16

In each simulation, the total proportion of the plot disturbed each year was set at 0.15, R0 was set to 1 and a further parameter, R_{max} (maximum patch size) was introduced to prevent the entire plot being obliterated. While this may occur occasionally in nature, the object here was to examine the impacts of disturbance without resetting the entire plot. R_{max} was set at 100 cm radius, or 22133 cm^2 planar area. For each value of *a*, ten replicate simulations were run, each for a duration of 200 years. Percent cover was taken from the model every year, while the size structure of species populations were taken at 200 years, as was the relative importance of total and partial mortality by coral group. For the initial 20 years, the number and size of disturbed patches was output from each replicate, in order to

determine whether limiting the maximum patch size had an influence on the overall area of plot disturbed each year.

3.2.4.2. Differential mortality probability

On the assumption that coral species vary in their susceptibility to disturbances (see Assumptions Section 3.2.1, point 6), a mortality probability was assigned for each coral species. *Agaricia* spp. has the highest tissue turnover rates (Bak and Luckhurst, 1980; Hughes and Jackson, 1985), so was assigned a probability of 1, (death occurs in all cases of disturbance impact). All other coral groups had probabilities of mortality less than *Agaricia* spp., and were set relative to rates of mortality of the latter. Differential mortality probabilities were based partly on colony size, a highly species-specific characteristic (Meesters et al., 2001; Soong, 1993), and rates of tissue regeneration (Appendix 2.4). For these life history traits, each coral was assigned a rank on a scale of 1 to 5, and differential mortality probabilities were based on the mean rank (Table 3.3). The range of probabilities fell between 1 (*Agaricia* spp.) and 0.1, signifying death as an outcome in 10% of disturbance impacts. In order to prevent some species from becoming extinct where little was known on which to base probabilities except for colony size, the probability of mortality was decreased (e.g. *Eusmilia fastigiata* and *Madracis* spp.)

Table 3.3 Differential mortality probabilities for ten coral species. These correspond to the chance of mortality during disturbance if impacted by a disturbed patch. Probabilities were based on colony size and rates of tissue regeneration.

Coral group	Mortality probability
Montastraea cavernosa	0.7
Stephanocoenia michelinii	0.1
Agaricia spp.	1
Eusmilia fastigiata	0.5
*Meandrina meandrites**	0.7
Montastraea annularis	0.6
Colpophyllia natans	0.3
Porites astreoides	0.2
Madracis spp.	0.1
Siderastrea siderea	0.1

* The mortality probability for this species was increased on the basis that these corals have been recorded as highly susceptible to mortality (Bak and Luckhurst, 1980).

Simulations were run to test the influence of differential mortality of coral species on coral community structure. The proportion of the plot affected by disturbance was 0.15 per year, using a value for powerlaw constant a of 1.5. All simulations were

initiated from bare substratum and run for 200 years, with 10 replicates of each set-up. Output in terms of percent cover was taken throughout the simulation.

3.3. Results

3.3.1. Proportion of the plot disturbed

The modelled coral community, run without any disturbance underwent a succession process whereby initially *Agaricia* spp. rapidly grew to occupy almost all space (90.9 ± 0.3%, mean ± 1 SD, n = 10) by 7 years (Figure 3.2). This group was out-competed by *Montastraea annularis,* and by 50 years, 87.8 ± 2.1% of the plot was covered by this species complex. However, *Montastraea cavernosa,* the competitively dominant species, ultimately out-competed *M. annularis* and dominated the plot. This succession process was complete by 272 years.

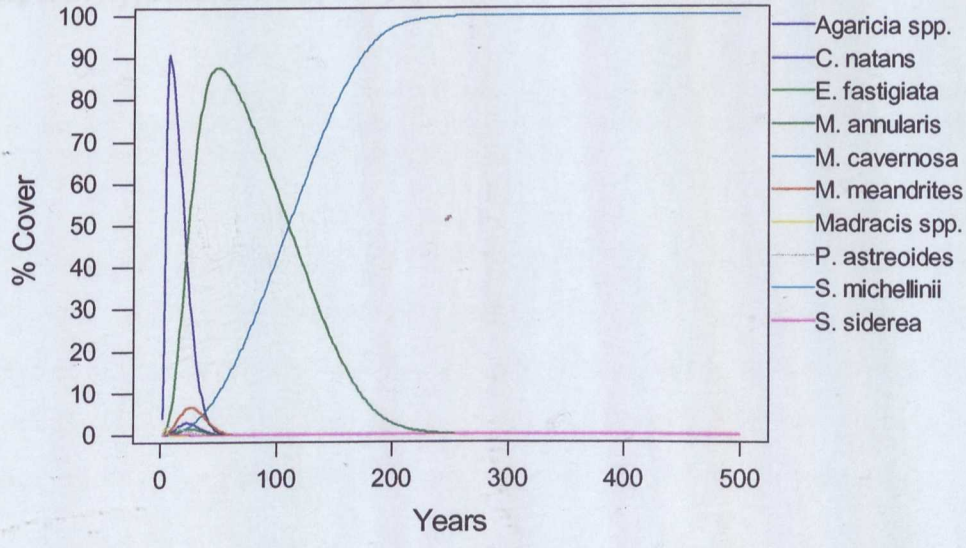


Figure 3.2 Community composition of modelled plot run without background disturbance (mean of 10 replicates).

The proportion of the plot impacted per year influenced both rate of community development and final community structure at 500 years (Figure 3.3). When 0.1 of

the plot was impacted, a succession process similar to that without disturbance occurred, but in this case, two species survived until the end of the simulation, *M. cavernosa* and *Agaricia* spp. (62.2 ± 0.5% and 12.6 ± 0.6% respectively, mean ± 1 SD, n = 10). When the proportion of the plot impacted year^{-1} was raised to 0.2, a greater species diversity was maintained, composed of four species: *M. cavernosa* was spatially dominant at 27 ± 0.5%, followed by *M. meandrites* at 21.5 ± 1.17%, and low abundances of *M. annularis* and *Agaricia* spp. were also present (8.3 ± 0.5% and 6.4 ± 0.4% respectively, mean ± 1 SD, n = 10). The simulation started with the same pattern in terms of an initial increase in *Agaricia* spp., followed by *M. annularis*, but the final stage in the community development was an increased abundance of *M. meandrites*. Proportions of the plot disturbed above this threshold led to entirely different communities; at 0.4 of the plot disturbed, there were initial peaks in *Agaricia* spp., followed by dominance by *M. meandrites* (36.3 ± 0.8%). Cover of *Agaricia* spp. subsequently declined to around 5%, similar levels to *M. annularis* (7.5 ± 0.4). At 0.6 of the plot impacted year^{-1}, the result was a community composed of two species, *M. meandrites* and *Agaricia* spp. (19.1 ± 0.5% and 8.8 ± 0.5% respectively, mean ± 1 SD, n = 10).

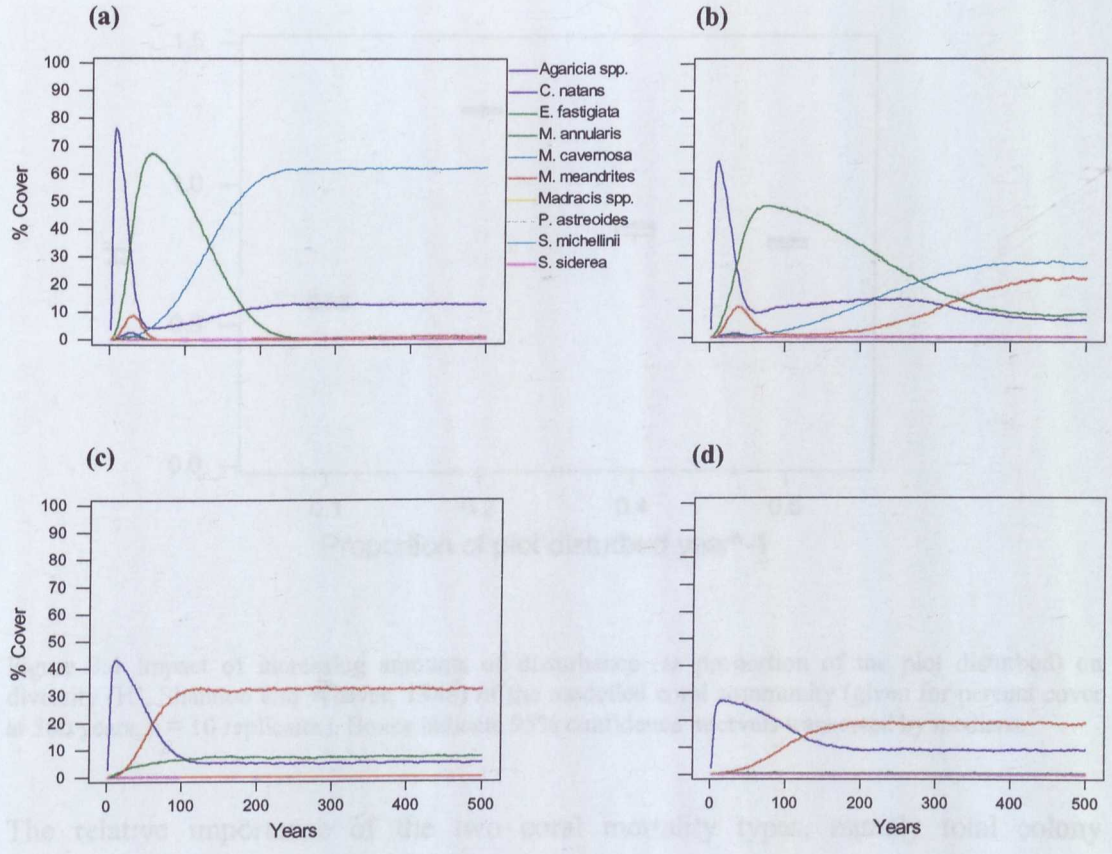


Figure 3.3 Effect of increasing proportions of the plot disturbed each year on modelled coral community composition. Disturbance was distributed in patches of 5 cm radius. (a) 0.1, (b) 0.2, (c) 0.4 and (d) 0.6 of the plot impacted year^{-1}. Mean of 10 replicates.

Diversity also responded to changes in the amount of disturbance (Figure 3.4). Diversity was highest at intermediate levels of disturbance, specifically at a proportion of 0.2 of the plot disturbed per year. Lower levels of disturbance led to spatial monopolisation by *M. cavernosa*, thereby decreasing diversity, while higher levels resulted in low abundance of all coral species apart from *M. meandrites* and *Agaricia* spp.

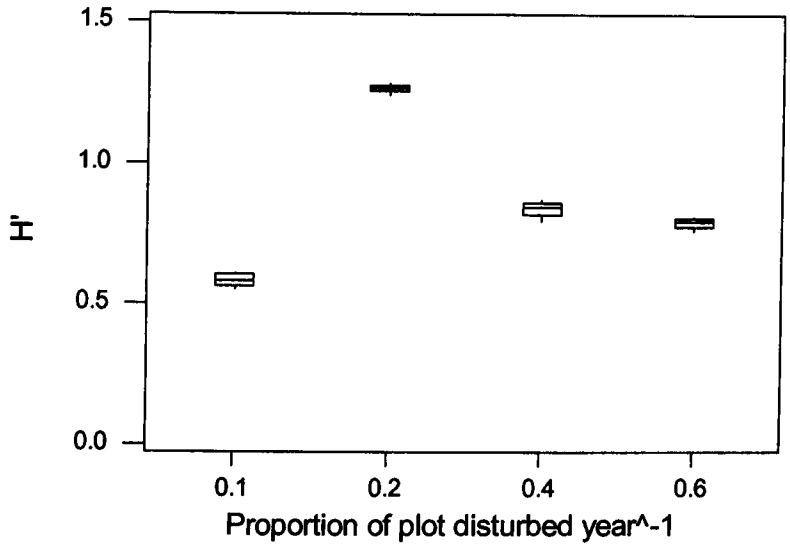


Figure 3.4 Impact of increasing amounts of disturbance (as proportion of the plot disturbed) on diversity (H', Shannon and Weaver, 1948) of the modelled coral community (given for percent cover at 500 years, n = 10 replicates). Boxes indicate 95% confidence intervals transected by medians.

The relative importance of the two coral mortality types, namely total colony mortality and partial mortality (shrinkage), was quantitatively assessed. A pattern emerged indicating that total colony mortality was relatively more important within small colony size classes, and partial colony mortality more important in larger size classes (Figure 3.5). This pattern was not influenced by the amount of plot disturbed. Four species were investigated in this way. Other species did not have sufficiently large populations to carry out this analysis, but all showed similar trends. The modal size class for colonies of each species also showed little response to increasing intensities of disturbance, though variability in the results obscures interpretation. In general though, modal colony size class appeared to be one to two size classes larger than the threshold between predominantly total colony mortality and predominantly partial colony mortality. This threshold fell in approximately the same position for all the species investigated, namely between size classes 3-6 and 7-19 cm^2.

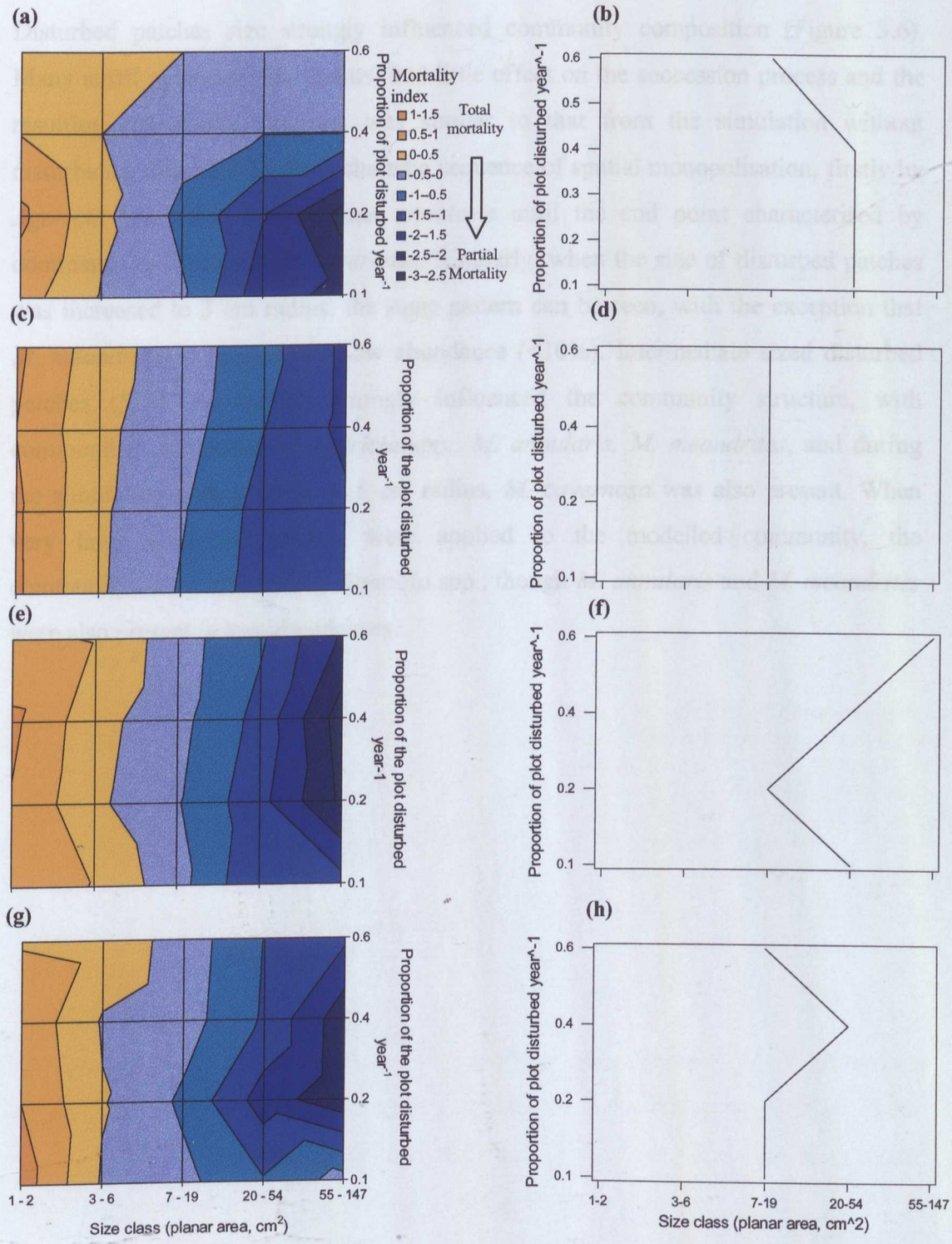


Figure 3.5 Effect of increased disturbance (proportion of the plot affected increased, patch sizes held constant) on relative importance of total vs. partial colony mortality and modal colony size. Mortality index is given as Log_{10} (# colonies with total mortality/# colonies with partial mortality), warm colours indicates a higher proportion of total to partial mortality while cold colours indicate more partial colony mortality. (a) and (b) *Montastraea cavernosa*, (c) and (d) *Agaricia* spp., (e) and (f) *Meandrina meandrites*, (g) and (h) *Montastraea annularis*. All graphs show cumulative population size structure for 10 replicates at 500 years.

3.3.2. Size of disturbed patches

Disturbed patches size strongly influenced community composition (Figure 3.6). Many small patches (1 cm radius) had little effect on the succession process and the resulting community structure was similar to that from the simulation without disturbance (Figure 3.2). Both shared a sequence of spatial monopolisation, firstly by *Agaricia* spp., then *Montastraea annularis* until the end point characterised by dominance of *Montastraea cavernosa.* Similarly, when the size of disturbed patches was increased to 3 cm radius, the same pattern can be seen, with the exception that *M. meandrites* is present at a low abundance (<10%). Intermediate sized disturbed patches (5-10 cm radius) strongly influenced the community structure, with communities composed of *Agaricia* spp., *M. annularis, M. meandrites*, and during the simulation with patches of 5 cm radius, *M. cavernosa* was also present. When very large disturbed patches were applied to the modelled community, the community was dominated by *Agaricia* spp., though *M. annularis* and *M. meandrites* were also present in low abundances.

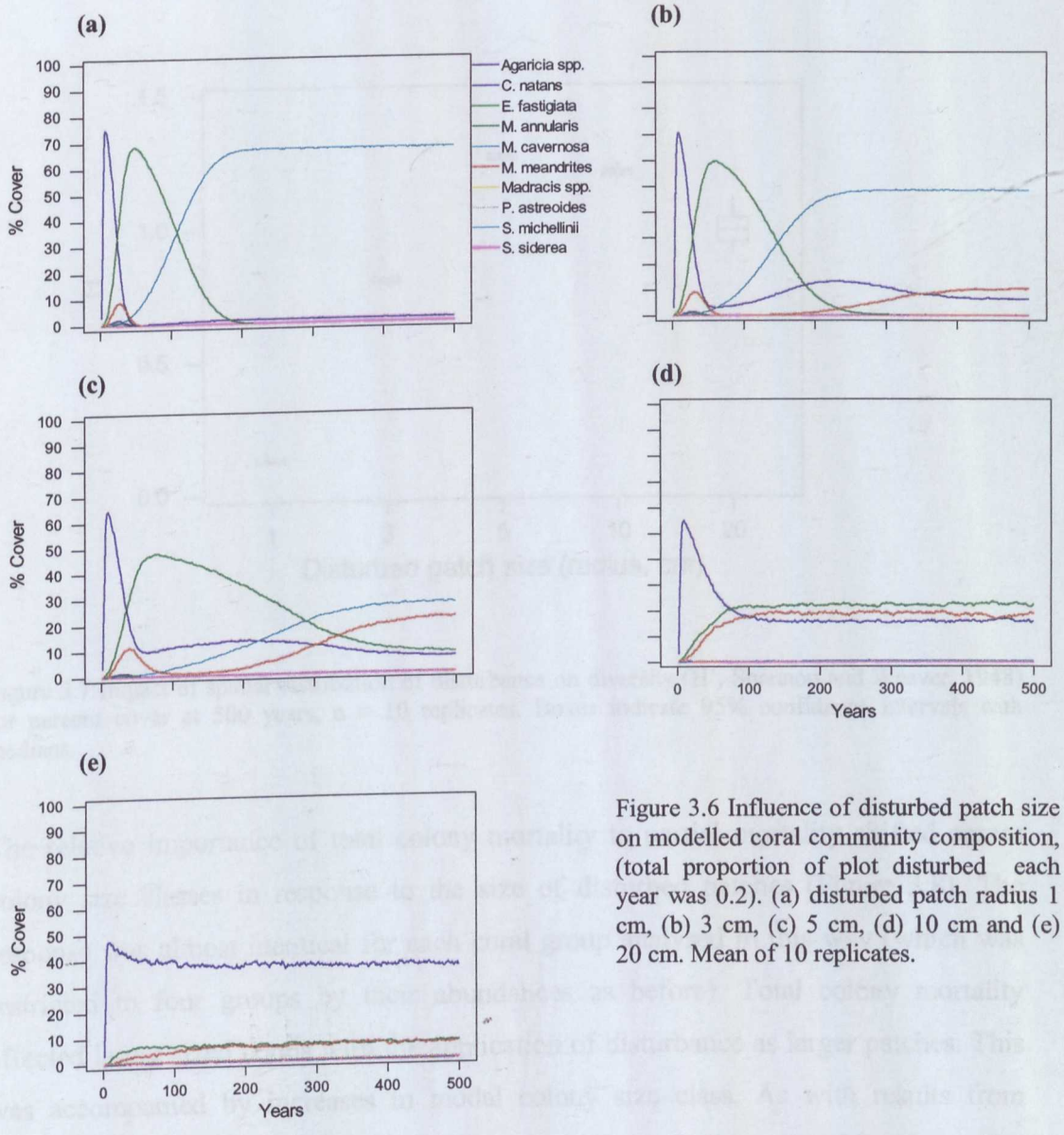


Figure 3.6 Influence of disturbed patch size on modelled coral community composition, (total proportion of plot disturbed each year was 0.2). (a) disturbed patch radius 1 cm, (b) 3 cm, (c) 5 cm, (d) 10 cm and (e) 20 cm. Mean of 10 replicates.

Patch size also influenced diversity of the modelled plot (Figure 3.7). Diversity was highest when disturbance impacted as intermediate sized disturbed patches. Small patches (1 cm radius) strongly decreased diversity, while very large patches (10 cm and 20 cm radius) also led to decreased diversity levels.

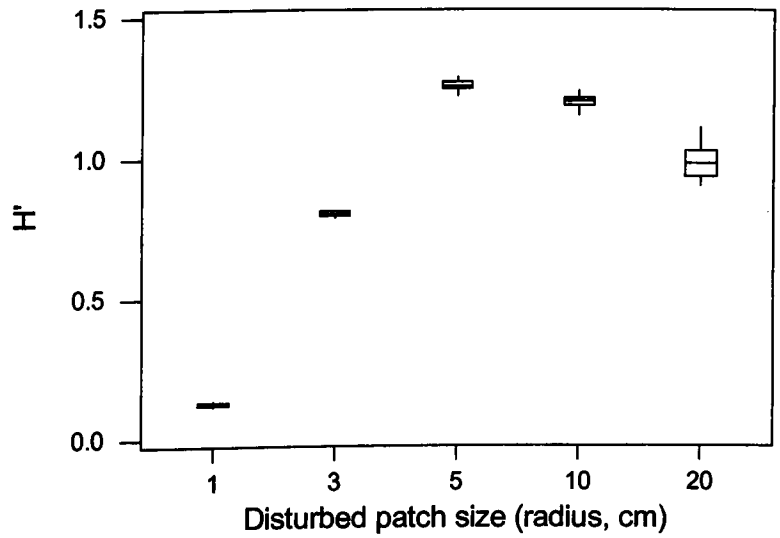


Figure 3.7 Impact of spatial distribution of disturbance on diversity (H', Shannon and Weaver, 1948) for percent cover at 500 years, n = 10 replicates. Boxes indicate 95% confidence intervals with medians.

The relative importance of total colony mortality to partial mortality shifted across colony size classes in response to the size of disturbed patches (Figure 3.8). The response was almost identical for each coral group analysed in this way (which was restricted to four groups by their abundances as before). Total colony mortality affected larger sized corals with the application of disturbance as larger patches. This was accompanied by increases in modal colony size class. As with results from varying the proportion of the plot of disturbance, modal size class of coral colonies was larger than the threshold colony size between predominately total mortality processes and predominately partial mortality.

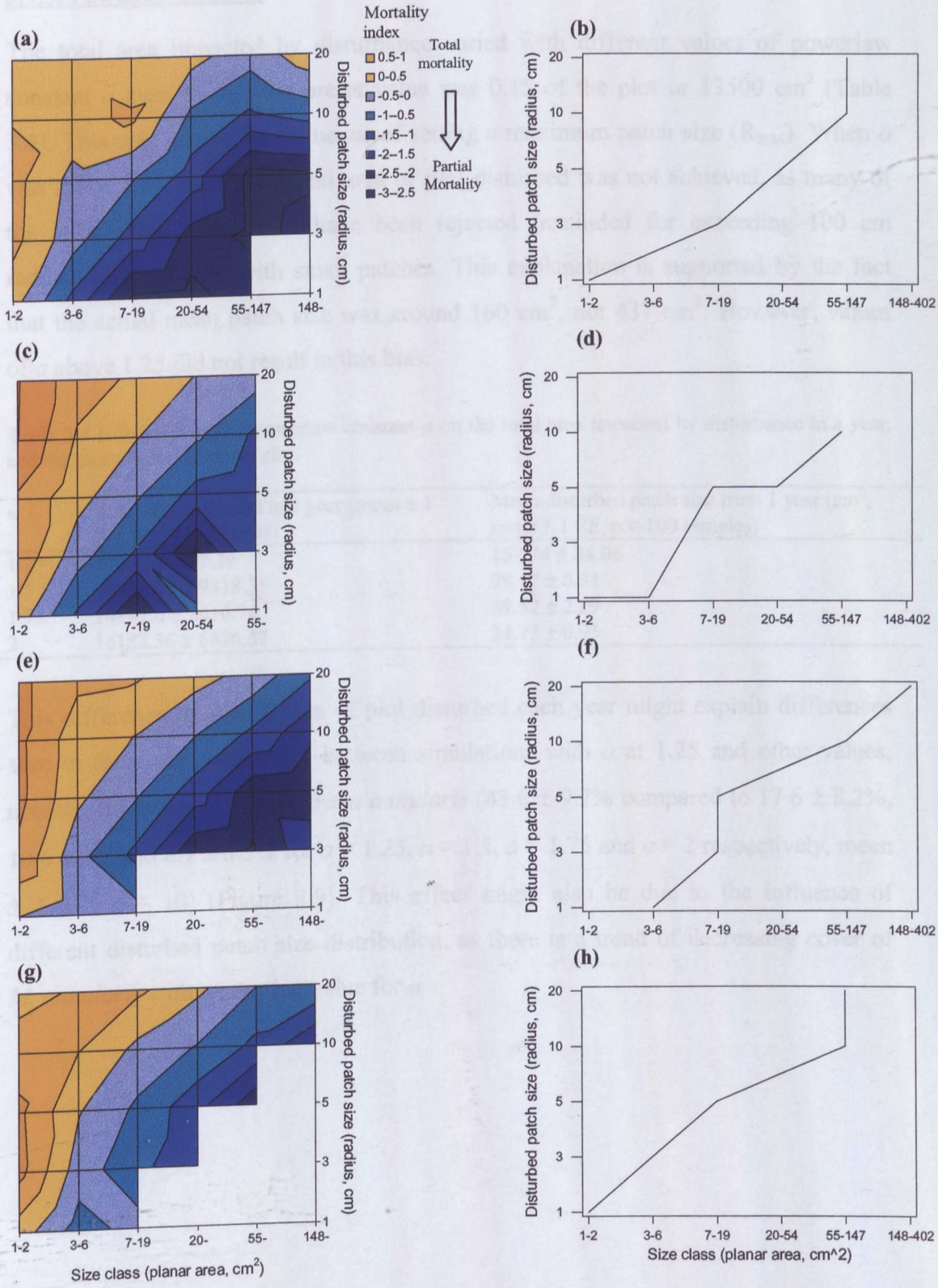


Figure 3.8 Influence of size of disturbed patch on relative importance of total vs. partial colony mortality and modal colony size. Mortality index is given as Log_{10} (# colonies with total mortality/# colonies with partial mortality), warm colours indicates a higher proportion of total to partial mortality while cold colours indicate relatively higher partial colony mortality. (a) and (b) *Montastraea cavernosa*, (c) and (d) *Agaricia* spp., (e) and (f) *Meandrina meandrites*, (g) and (h) *Montastraea annularis*. All graphs show cumulative size structure for 10 replicates at 500 years.

3.3.3. Powerlaw function

The total area impacted by disturbance varied with different values of powerlaw constant *a* even though the preset value was 0.15 of the plot or 13500 cm^2 (Table 3.4). This was due to the influence of setting a maximum patch size (R_{max}). When *a* was set at 1.25, the preset total area of plot disturbed was not achieved, as many of the large patch sizes must have been rejected (excluded for exceeding 100 cm radius), and replaced with small patches. This explanation is supported by the fact that the actual mean patch size was around 160 cm^2, not 437 cm^2. However, values of *a* above 1.25 did not result in this bias.

Table 3.4 Effect of varying powerlaw constant *a* on the total area impacted by disturbance in a year, and the mean disturbed patch size.

a	Total area impacted in 1 year (mean ± 1 SD, n = 100 samples)	Mean disturbed patch size from 1 year (cm^2, mean ± 1 SE, n = 100 samples)
1.25	4792.2 ± 677.29	159.74 ± 24.06
1.5	10925.84 ± 9318.35	79.17 ± 6.31
1.75	14187.6 ± 8616.74	39.52 ± 2.29
2	16182.36 ± 6696.53	24.73 ± 0.95

This difference in overall area of plot disturbed each year might explain differences seen in the coral community between simulations with *a* at 1.25 and other values, notably, the cover of *Montastraea annularis* (43.6 ± 9.7% compared to 17.6 ± 8.2%, 10.6 ± 3.2 and 8.9 ± 3.3% for $a = 1.25$, $a = 1.5$, $a = 1.75$ and $a = 2$ respectively, mean ± 1 SD, n = 10) (Figure 3.9). This effect might also be due to the influence of different disturbed patch size distribution, as there is a trend of decreasing cover of *M. annularis* with increasing value for *a*.

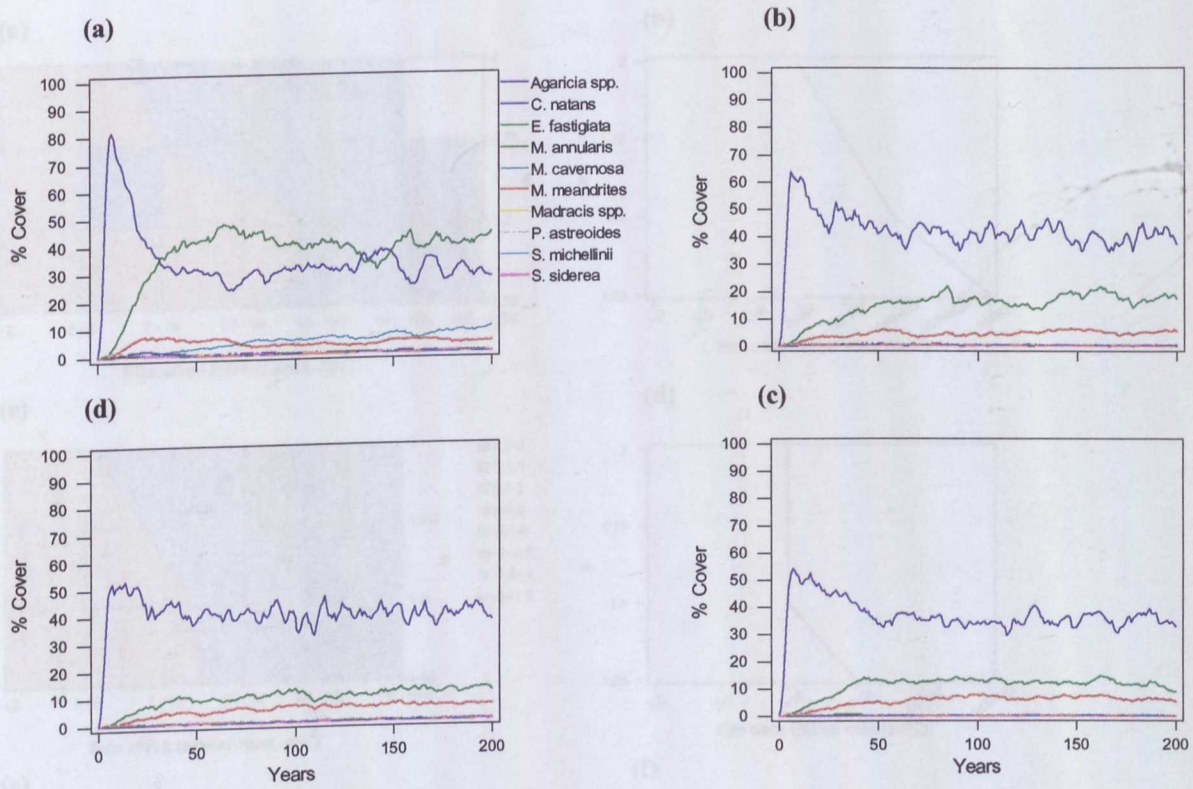


Figure 3.9 Influence of powerlaw constant a on modelled coral community composition. (a). $a = 1.25$, (b) $a = 1.5$, (c) $a = 1.75$ and (d) $a = 2$. Mean of 10 replicates.

The relative importance of total colony mortality compared to partial mortality shifted from larger to smaller size classes with increasing values for a (Figure 3.10). Total colony mortality affected the largest colony sizes when a was set at 1.25, when the greatest proportion of large disturbed patches were generated. Modal colony size class followed the same trends as the threshold between total and partial colony mortality, though for *M. meandrites* this trend appears to be obscured by variability within results.

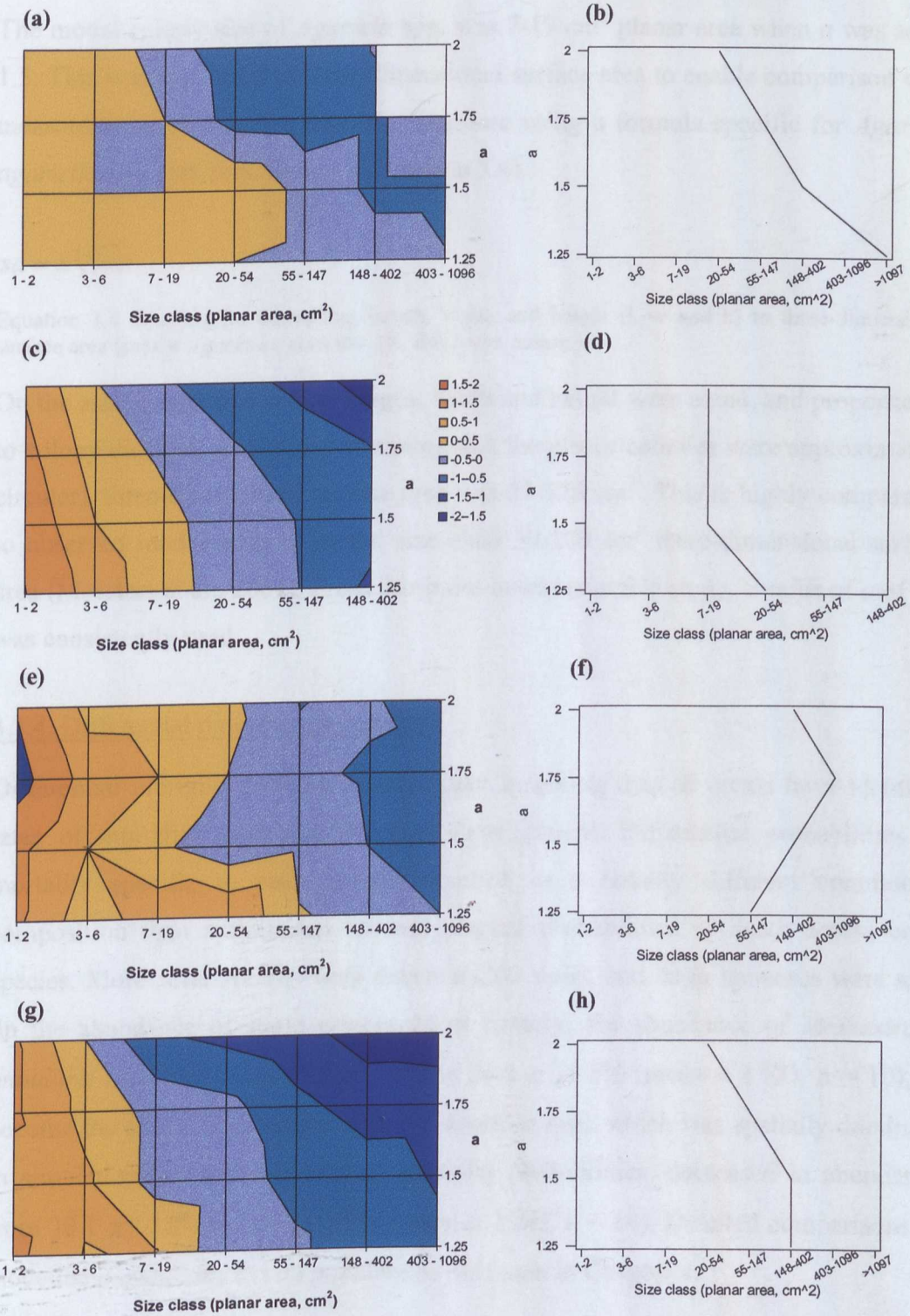


Figure 3.10 Influence of powerlaw constant *a* on relative importance of total vs. partial colony mortality and modal colony size. Mortality index is given as Log_{10} (n colonies with total mortality/n colonies with partial mortality), warm colours indicates a higher proportion of total to partial mortality while cold colours indicate relatively higher partial colony mortality. (a) and (b) *Montastraea cavernosa*, (c) and (d) *Agaricia* spp., (e) and (f) *Meandrina meandrites*, (g) and (h) *Montastraea annularis*. All graphs show cumulative size structure for 10 replicates at 200 years.

3.3.3.1. Determining the most appropriate value for *a* for this model

The modal colony size of *Agaricia* spp. was 7-19 cm^2 planar area when *a* was set at 1.5. This was converted to three-dimensional surface area to enable comparison with measurements of colonies from the literature using a formula specific for *Agaricia agaricites* (R. Bak pers. comm.) (Equation 3.4).

$$sa = \pi\sqrt[3]{lwh}$$

Equation 3.4 Formula for converting length, width and height (l, w and h) to three-dimensional surface area (sa) for *Agaricia agaricites*, (R. Bak, pers. comm.).

On the assumption that colony length, width and height were equal, and proportional to colony diameter (calculated assuming that the planar colonies were approximately circular), three-dimensional surface area was 27-124 cm^2. This is highly comparable to observed modal sizes of modal size class 30-100 cm^2 three-dimensional surface area (Meesters et al., 2001). From this point onwards in this study, a value of *a* of 1.5 was consistently used.

3.3.4. Differential mortality probability

Differential mortality is more realistic than assuming that all corals have identical rates of mortality, and was the next development. Differential probabilities of mortality specific to each species resulted in a notably different community composition than simulations assuming equal probabilities of death across coral species. More coral species were extant at 200 years, and large increases were seen in the abundance of some groups. Most notably, the abundance of *Montastraea annularis* increased from 17.2 ± 7.6% to 36.4 ± 11.5% (mean ± 1 SD, n = 10), to become the spatially dominant species. *Agaricia* spp., which was spatially dominant in simulations without differential mortality probabilities, decreased in abundance from 39.1 ± 12.2% to 20.8 ± 7.9% (mean ± 1 SD, n = 10). Detailed comparisons of modelled populations to real populations are made in Chapter 4.

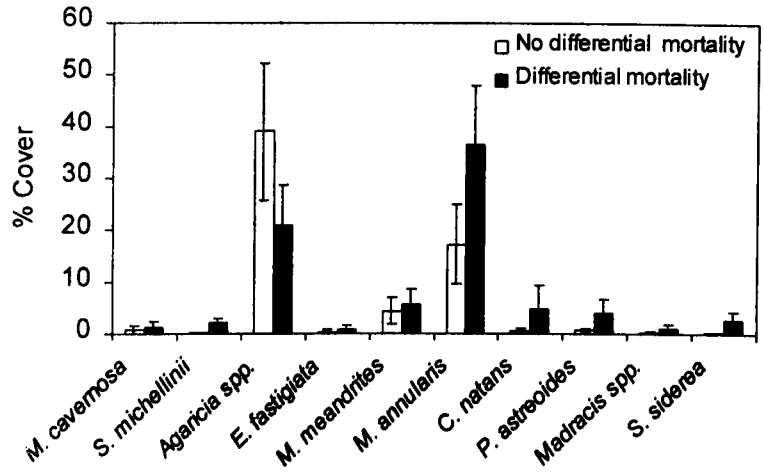


Figure 3.11 Composition of the modelled community from simulations run with and without differential mortality probabilities. Percent cover taken at 200 years, mean ± 1 SD, n = 10 replicates.

3.4. Discussion

Disturbance is a strong structuring force in coral communities, and its influence is reflected by this model. Initial work investigating the amount and size of disturbed patches showed that both these parameters strongly influenced the coral community. This was used as the foundation for implementing a powerlaw model.

The proportion of the plot disturbed had a strong effect on both the composition of the modelled coral community and diversity. At both very low and very high levels of disturbance, low species diversity was observed, but different species were represented in each of these situations. At low disturbance levels, the competitively dominant species, *Montastraea cavernosa*, monopolised the plot while at high disturbance levels ephemeral coral groups such as *Agaricia* spp. dominated the plot. This supports the long held concept that diversity becomes highest at intermediate disturbance levels (Connell, 1978).

The size of disturbed areas was equally important in structuring the coral community. This reflects the relative importance of two mechanisms for recolonisation of newly created space: 1) new recruitment and 2) growth and repair of colony fragments surviving disturbance at the edge of the patch. Small patches are predominately

recolonised by surviving corals while large patches open up space for recruitment (Connell and Keough, 1985). This explains the observed pattern of increasing diversity with increasingly large disturbed patches even when the overall area disturbed is constant, for example, as *Montastraea cavernosa* rapidly regenerated tissue lost in small patches, with little impact on its overall monopolisation of the plot. Intermediate sized patches generate a temporal mosaic (*sensu* Grassle, 1973), whereby different patches of the plot were at different stages of succession. Very large patches prevent the establishment of species with low rates of tissue turnover (i.e. low rates of growth and recruitment), and provided a suitable environment for only the most ephemeral species. This highlights the importance of the manner in which disturbance is spatially distributed. In practice, this is rarely measured, in preference simple cover measurements are mostly used.

Large disturbed patches can kill relatively large colonies. Thus large patches drove the modal colony size class to larger sizes. This relationship between modal colony size and the relative importance of different mortality processes acting to structure the population has been suggested by Bak and Meesters (1998). These results clearly demonstrate a relationship exists though the modal size class in all cases fell around one size class larger than the threshold size between the relative importance of total colony mortality and partial colony mortality. This has implications regarding our understanding of the age structure of corals as colonies of the modal size will be susceptible to partial mortality, along with those just smaller, and thus the relationship between size and age is likely to be decoupled at smaller sizes than previously thought (Bak and Meesters, 1998). Increasing our understanding of mortality processes structuring a population also yields insight into the pattern of other size dependant processes, namely fecundity, which is strongly related to colony size (Soong, 1993).

This relationship between disturbance patch size and modal colony size class was used to parameterise disturbance using a powerlaw model. The constant controlling the shape of the model, a, shifted the relative importance of total colony mortality to partial mortality. This in turn influenced the modal size class of the population. By comparing the size structure of modelled populations under different values of a for *Agaricia* spp. to those from the literature, the coral group with the highest tissue

turnover, the most appropriate value for *a* was determined (1.5 yielded a population with a modal size class of 27-124 cm^2 three-dimensional surface area). The validity of this technique to estimate rates of background disturbance within populations of *Agaricia* spp. is strengthened by two further facts; 1) increasing the overall area of the plot affected by disturbance will not affect the population size structure of *Agaricia* spp., as demonstrated earlier, in the investigation into the effects of increasing proportions of the plot affected by disturbance (though this is likely to influence population density) and 2) population size structure is a highly stable species-specific character (Meesters et al., 2001; Soong, 1993).

Using a powerlaw model to assign patch sizes is a more informative and intuitive method for managing background mortality processes within the model than dividing corals into colony size classes and assigning them rates of total colony and partial mortality. Interestingly, where the latter was done for *Porites* spp. (Done, 1988), a parameter was included that described the maximum size for colonies suffering total colony mortality, which is analogous to the threshold between total and partial mortality in this model, though in this case it is an outcome of disturbance regime, not a preset parameter of the model.

Introducing differential probabilities of mortality for coral species enabled the co-persistence of a larger number of species. There is a great deal of evidence to suggest that *Agaricia* spp. has the highest rates of mortality out of the species included here. *Agaricia* spp. have an extreme life history strategy, while at the opposite end of the spectrum are highly persistent species such as *Montastraea annularis*, which have been viewed as endpoints on a continuum with other species lying in intermediate positions (Hughes and Jackson, 1985). While this view does not take into account species that have contrasting reproductive strategies, such as *Acropora palmata*, via fragmentation of branching colonies during storms leading to asexual propagation (Bak and Meesters, 1997; Highsmith, 1982; Highsmith et al., 1983), it does provide a framework within which to consider the functionality of coral species.

Colony size was used as an indicator to determine the relative probability of a coral species suffering mortality. Growth was considered indeterminate (*sensu* Sebens, 1987), and the size a colony attained at any particular time was a function of the

processes acting on it. No assumption regarding the genetic constraint of colony size was made.

Chapter 4. Parameter testing

4.1. Objectives

In this chapter, the sensitivity of the model to each of the life history parameters is tested. Two further areas are investigated, namely the influence of interactive reach (spatial range of competitively interacting corals), and temporal variability in supply of coral larval to the plot.

This was undertaken in part to identify influences to model output and also to establish the range of conditions under which the model may be considered reliable. Knowledge of the reliability of the model is especially important as parameter values were extracted from many sources, that in turn come from a range of geographical locations in the Western Atlantic, different environmental regimes, and from different researchers using varying methodologies (Appendix 2.2). Another aspect of sensitivity testing is that this enables further understanding of how parameters operate in coral life history strategies, and how these in turn may mediate individual species sensitivities to parameter changes.

Finally, the chapter quantifies the influence of two structuring processes that potentially could be important, namely interactive reach and temporal variability in supply of recruits. Interactive reach can be defined as the distance between the retracted tissue of a dominant coral and the nearest living tissue of a subordinate (Sheppard, 1982). On reefs it is manifest as a halo of bare substratum around coral colonies, which is maintained by aggressive mechanisms of corals acting to retain space for the colony and prevent encroachment by other organisms. Such mechanisms include the extrusion of mesenterial filaments, development of specialised sweeper tentacles and sweeper polyps and histo-incompatibility responses (Lang and Chornesky, 1990). While the role of competition in structuring reef communities has been disputed (Bradbury and Young, 1981; Sheppard, 1979), it

remains that a large proportion of 'empty' space on a reef may not actually be available for colonisation, e.g. for subordinate species.

Larval recruitment is highly variable (Hughes et al., 1999; Sammarco, 1991; Connell et al., 1997; Hughes, 1985). Biological and physical factors affect it, such as substratum availability, fecundity, reproductive mode and regional oceanography (Babcock, 1988; Harriott and Fisk, 1987). It is important to know whether species frequencies are limited by numbers of settling larvae. If they are, coral community structure will reflect temporal patterns of larval availability. Alternatively, post-settlement mortality processes could be more important in mediating the influence of variability in larval supply, and so may hold a more important role in structuring the coral community.

4.2. Methods

4.2.1. Parameter sensitivity

The modelled coral community was tested for sensitivity to coral life history parameters. Growth, recruitment, mortality and competitive rank were varied individually for each species, within and beyond the range that which these variables are known to operate. For each life history parameter, three or four values were tested, both above and below the initial value (Table 4.1).

Table 4.1 Changes in life history parameter values used in sensitivity test.

Life history parameter	Levels
Growth	Baseline rate was multiplied by factors of 0.5, 1.1, 1.5 and 2
Recruitment	Baseline rate was multiplied by factors of 0.5, 1.1, 1.5 and 10
Relative mortality probability	Increments of 0.1 and 0.3 were added to the baseline probability (except for *Agaricia* spp. in which these increments were subtracted from its baseline probability) [1]
Aggressive rank	Increments of 1, 2 and 3 were added to all ranks (apart from *Montastraea cavernosa* (-1, -2, -3), *Montastraea annularis* (1, -1, -2) and *Meandrina meandrites* (1, 2, -1)) [2].

[1] Unlike other species, the differential mortality probability for *Agaricia* spp. was decreased, as further increases to the baseline value of 1 would not have yielded a probability.
[2] Competitively dominant species had their competitive ranks reduced.

Model conditions are given in Table 4.2. At 100 years output was taken as percent cover, the number and size of colonies, correlation coefficients were calculated using

mean percent cover from the ten replicates, and responses by species were quantified using this relationship if it was clearly linear (confirmed by fits vs. residuals plots).

Table 4.2 Model conditions.

Condition	Setting
Species attributes*	As Table 3.1
Starting conditions	Bare substratum
Disturbance settings (see Chapter 3)	0.15 of the plot disturbed each year, a = 1.5, R_{max} = 100, R0 = 1.
Results output	At 100 years
Number of replicates of each simulation	10

* These were baseline values for parameter sensitivity testing.

Finally, in order to try and quantify which life history parameters most strongly influenced relative abundance, and which species were most sensitive to changes in parameter values, sensitivities were normalised relative to each other by converting real values to ranks. A sensitivity rank of 1 indicated a relative change in percent cover of 0 to 5%, a rank of 2, 5 to 10% change and 3, >10% change. Results were compared for increases of two-fold for growth and recruitment rates, and increases of 0.1 and 1 for differential mortality probabilities and competitive rank respectively. Ranks were averaged across species for each life history parameter, and across parameters for each species.

4.2.2. Interactive reach

The interactive reach of coral species was measured when assessing the aggressive competence of corals (see Section 3.2.2. for description of methods) from reef slopes between 10-20 m at Utila, Honduras. For each pair of interacting coral species, the dominant and subordinate were established, and the interactive reach of the dominant coral was measured as the narrowest point between colonies (*sensu* Sheppard, 1982). The average value for each coral species was taken as the parameter value (Table 4.3).

Table 4.3 Values for interactive reach (distance over which corals interact) obtained by field measurement in Utila, Honduras.

Species	Interactive reach (cm)
Montastraea cavernosa	2.07
Stephanocoenia michelinii	0.38
Agaricia spp.	0.38
Eusmilia fastigiata	1.3
Meandrina meandrites	1.5
Montastraea annularis	1.26
Colpophyllia natans	1.2
Porites astreoides	0.47
Madracis spp.	0.7
Siderastrea siderea	0.43

A module was written to simulate the action of corals in maintaining a region of bare substratum around their colonies, according to 1) aggressive rank and 2) interactive reach.

Simulations were run with and without the interactive reach module, with model conditions as previously (Table 4.2). In order to assess the influence of interactive reach on juvenile dynamics, the model tracked the cohort recruiting at year 100, and density by species was taken at settlement, and every subsequent year up to 4 years from settlement.

Coral communities were compared using Bray-Curtis similarity matrices (Bray and Curtis, 1957) using untransformed percent cover data at 100 years for all 10 replicates. One-way ANOSIM (analysis of similarity, Clarke, 1993) was used to compare coral communities from simulations with and without the interactive reach module.

Average juvenile density data were converted into survivorship values between settlement and the end of the first year. Survivorship was compared between simulations with and without interactive reach, where sufficient recruitment occurred.

4.2.3. Temporal variability in recruitment

To assess the effect of temporal variability in larval supply on the model, the influence of five probability distributions for determining the availability of recruits were compared. These were variance: mean ratio of 1:1 (= Poisson distribution), and 4 increasing negatively binomial distributions (variance: mean ratios of 5:1, 10:1, 15:1 and 20:1). In each case the mean number of recruits was kept constant (Figure 4.1).

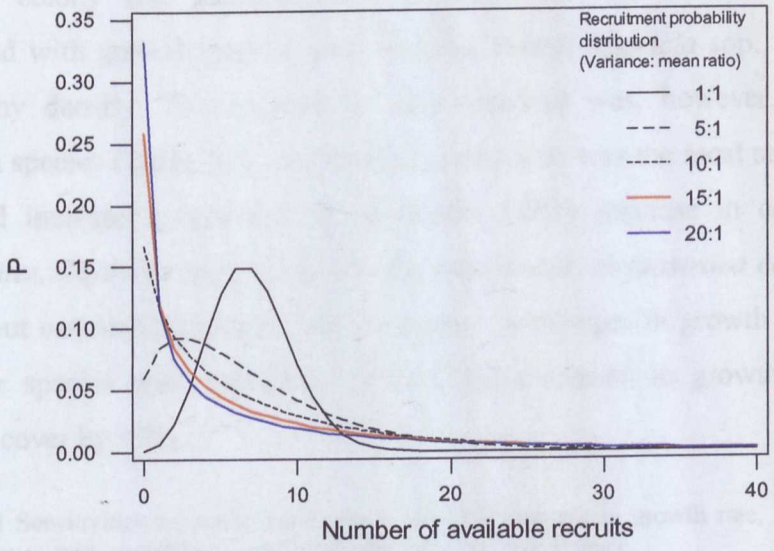


Figure 4.1 Poisson and negative binomial recruitment probability distributions (given as variance: mean ratio). P is the probability of getting a certain number of recruits. The mean rate of recruitment shown was 7 larvae 9 m^2 $year^{-1}$.

Model conditions were as shown in Table 4.2, and juvenile survivorship data were collected along with coral abundance (see Section 4.2.2). Bray-Curtis similarity matrices were constructed as before, and coral community structure was compared of between levels of larval temporal variability using a one-way ANOSIM. Differences in variance in community structure within replicates were assessed by carrying out Bartlett's test on cover at 100 years, across levels of recruitment variability of these communities. Variability in juvenile density was quantified by calculating the coefficient of variation at each life history stage.

4.3. Results

4.3.1. Parameter sensitivity

4.3.1.1. Growth rate

All species demonstrated similar responses to increased growth rate, namely increased cover (Appendix 3.1). A linear relationship was found between cover and growth rate, although variability between replicates was high. This was simply because colony size increases with growth rate. The number of colonies also increased with growth rate for most species, except *Agaricia* spp., which decreased in colony density. The strength of this response was, however, highly variable between species (Table 4.4). *Montastraea annularis* was the most sensitive species; a two-fold increase in growth rate generated >20% increase in cover. *Meandrina meandrites, Agaricia* spp., *Colpophyllia natans* and *Montastraea cavernosa* showed lesser, but noticeable changes, but the impact of changes in growth rate on the cover of other species was negligible, as two-fold increases in growth rate influenced relative cover by <5%.

Table 4.4 Sensitivities of coral species to a two-fold increase in growth rate, given as increase in percent cover, with correlation coefficient and statistical significance.

Species	Relative % increase in cover	Pearson correlation coefficient (r) for cover against growth rate	p
M. annularis	24.79	0.973	0.005
M. meandrites	13.94	0.941	0.017
Agaricia spp.	10.64	0.929	0.023
C. natans	8.18	0.996	<0.001
M. cavernosa	6.67	0.98	0.003
S. michelinii	4.42	0.968	0.007
P. astreoides	4.35	0.944	0.016
S. siderea	3.80	0.946	0.015
E. fastigiata	2.97	0.963	0.009
Madracis spp.	1.45	0.985	0.002

4.3.1.2. Recruitment rate

All species increased in abundance with increased rates of recruitment (Appendix 3.2). As would be expected, the number of colonies increased, but the size of

colonies in most species decreased. Exceptions to this general rule were *Eusmilia fastigiata* and *Madracis* spp., which had no obvious relationship between colony size and recruitment rate.

The range of sensitivity values was low, indicating a low overall sensitivity of model output to changes in recruitment rate (Table 4.5). The most sensitive species was *Montastraea annularis*, which increased in relative cover by only 2% with a two-fold increase in recruitment rate. Other species that also increased in cover by >1% were *Porites astreoides*, *Montastraea cavernosa*, *Meandrina meandrites*, *Agaricia* spp. and *Stephanocoenia michellenii*. For most species, the relationship between cover and recruitment rate was linear, but notable exceptions were *Montastraea annularis* and *Agaricia* spp., which were also the species to show the greatest declines in colony size.

Table 4.5 Sensitivities of coral species to a two-fold increase in recruitment rate, given as percent increase in cover, with correlation coefficient.

Species	Sensitivity (% increase in cover)	Pearson correlation coefficient (r)	p
Montastraea annularis	2.07	0.077*	0.836
Porites astreoides	1.70	0.002	0.988
Montastraea cavernosa	1.58	0.006	0.969
Meandrina meandrites	1.35	0.005	0.975
Agaricia spp.	1.20	0.18*	0.709
Stephanocoenia michelinii	1.08	0.001	0.99
Colpophyllia natans	0.89	0.029	0.915
Eusmilia fastigiata	0.67	0.002	0.987
Madracis spp.	0.60	0	0.998
Siderastrea siderea	0.60	0.001	0.99

* non-linear response

4.3.1.3. Differential mortality probability

Increasing the differential mortality probability increased the chances of a coral dying if impacted by a disturbed patch. All coral species responded with decreases in cover (*Agaricia* spp. increased in cover with a decrease in its relative mortality probability, but the relationship was the same) (Appendix 3.3). This response proved to be strongly linear in all species. On the whole, colony size also decreased, but this trend was not clear for a number of species including *Montastraea cavernosa*, *Agaricia* spp., *Eusmilia fastigiata* and *Madracis* spp. Likewise, the number of colonies generally decreased, although again, trends were unclear in *M. cavernosa*

and *Madracis* spp., which appeared to be resistant to changes in the probability of mortality.

The strength of the relationship between differential mortality probability and abundance varied greatly between species (Table 4.6). Only two species had significant correlation coefficients, these were *Montastraea annularis* and *Agaricia* spp., and along with *Meandrina meandrites* and *Colpophyllia natans*, these were the only species to change in relative cover by >1%. All other species appeared to be resistant to changes in parameter values for relative mortality probability indicating an overall low sensitivity of the model to changes in this parameter.

Table 4.6 Sensitivities of coral species to a 0.1 increase in differential mortality probability, given as relative percent increase in cover, with correlation coefficient.

Species	Sensitivity (relative % increase in cover)	Pearson correlation coefficient (r)	P
Montastraea annularis	5.69	-0.998	0.035
Agaricia spp.	2.13	-0.999	0.026
Meandrina meandrites	1.17	-0.979	0.132
Colpophyllia natans	1.3	-0.944	0.213
Porites astreoides	0.796	-0.902	0.285
Siderastrea siderea	0.655	-0.921	0.255
Stephanocoenia michelinii	0.486	-0.985	0.111
Montastraea cavernosa	0.268	-0.624	0.571
Madracis spp.	0.138	-0.99	0.088
Eusmilia fastigiata	0.137	-0.944	0.214

4.3.1.4. Aggressive rank

Increases in the value of competitive ranks for any coral species resulted in increased cover (Appendix 3.4). This increase in cover was brought about by a combination of increased colony size and survival leading to an increased number of colonies. Some species were extremely sensitive to changes in their competitive rank, with changes of just one place in the hierarchy resulting in changes in cover from 3-fold (*Eusmilia fastigiata, Meandrina meandrites, Montastraea annularis, Porites astreoides*) to >5-fold (*Stephanocoenia michellenii, Madracis* spp. and *Siderastrea siderea*). This response was non-linear, so further analyses was not carried out. The reason for non-linearity was that initial ranking was not strictly hierarchical; several species shared ranks. Thus the transition of a species from one rank to another may be slightly beneficial if it then shared ranks with species occupying large proportions of the plot

and could prevent overgrowth, or extremely beneficial if it was able to outcompete such species.

4.3.1.5. Sensitivity comparison across life history attributes and species

Changes in competitive ranking resulted in a greater change in community composition than any other parameters. Growth was the second most influential parameter, with changes in rates of recruitment and mortality having least impact on the model (Table 4.7).

Species varied in their sensitivity to life history parameters, and broadly fell into two groups; 1) those that were sensitive to most parameters, e.g. *Montastraea annularis,* and 2) those that were resistant to changes in all parameters except competitive rank. It is interesting to note that the latter group was composed of subordinate species (all ranking below 5 in aggressive capacity, the midpoint rank of the hierarchy): *Stephanocoenia michellenii, Agaricia* spp., *Porites astroides, Madracis* spp. and *Siderastrea siderea.* This again reflects the importance of spatial competition, highlighting that even if rates of growth are changed but a species is low-ranking competitively, there is little overall impact on abundance.

Table 4.7 Relative sensitivity ranks by species to different life history traits. Sensitivity ranks were assigned according to changes in cover; 1 = 0-5% change, 2 = 5-10% change and 3 =>10% change. Results are given for value changes of two-fold for growth and recruitment rates, but 0.1 and 1 for differential mortality probability and competitive rank (as the latter response was non-linear, the largest increase in cover is given).

Species	Growth	Recruitment	Relative mortality	Competitive rank	Average by species
Montastraea annularis	3	1	2	3	2.25
Meandrina meandrites	3	1	1	3	2
Colpophyllia natans	2	1	1	1	1.25
Montastraea cavernosa	2	1	1	1	1.25
Agaricia spp.	2	1	1	2	1.5
Stephanocoenia michelinii	1	1	1	3	1.5
Eusmilia fastigiata	1	1	1	2	1.25
Siderastrea siderea	1	1	1	3	1.5
Porites astreoides	1	1	1	3	1.5
Madracis spp.	1	1	1	3	1.5
Average by parameter	1.7	1	1.1	2.4	

4.3.2. Interactive reach

Interactive reach of a coral had no detectible influence on coral community structure (Table 4.8, one-way ANOSIM on Bray-Curtis similarity matrices, global R = -0.068, p = 0.888), except that it influenced the survival of newly settled juvenile corals (Figure 4.2). Seven out of 10 species showed decreased juvenile survivorship under conditions where interactive reach was included. Four of these species were tested statistically, (as they had 8 or more observations) and significant differences were seen in survivorship of *Porites astreoides* juveniles (two-way T test: $T = 4.35_{(df = 18)}$, $p<0.001$), *Agaricia* spp. juveniles ($T = -6.49_{(df = 18)}$, $p<0.001$), but no differences were detected in *Montastraea annularis* juveniles ($T = 1.90_{(df = 17)}$, $p=0.074$), or *Madracis* spp. juveniles ($T = 1.84_{(df = 17)}$, $p = 0.083$).

Table 4.8 Community composition of plot at 100 years run with and without interactive reach (% cover, mean ± 1 SD, n = 10 replicates.

Species	Without interactive reach	With interactive reach
Montastraea cavernosa	10.10 ± 5.93	14.73 ± 3.14
Stephanocoenia michelinii	0.31 ± 0.28	0.26 ± 0.16
Agaricia spp.	13.97 ± 4.25	11.82 ± 5.60
Eusmilia fastigiata	0.17 ± 0.19	0.19 ± 0.24
Meandrina meandrites	1.39 ± 0.84	0.82 ± 0.65
Montastraea annularis	57.71± 5.61	50.98 ± 6.11
Colpophyllia natans	0.54 ± 0.60	0.36 ± 0.39
Porites astreoides	1.10 ± 0.43	0.65 ± 0.26
Madracis spp.	0.35 ± 0.19	0.22 ± 0.1
Siderastrea siderea	0.21 ± 0.08	0.20 ± 0.15

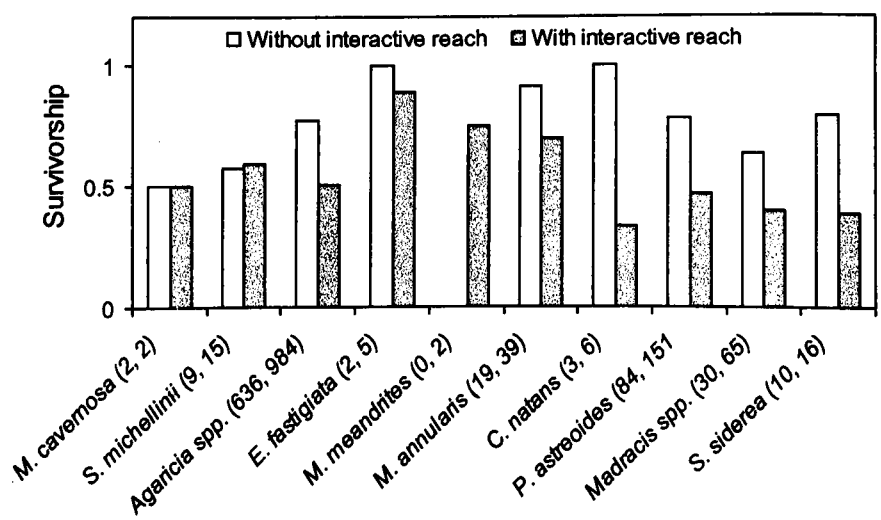


Figure 4.2 Effect of interactive reach on juvenile survivorship (from settlement to end of first year, as probability). Mean survivorship (total n larvae settled given in parentheses for runs without and with interactive reach respectively), n = 10 replicate simulations, output taken at 100 years.

4.3.3. Temporal variability in recruitment

Increasing the temporal variability in recruitment had no effect on community composition (one-way ANOSIM on Bray-Curtis similarity matrix results: global R = 0.025, p = 0.21). Variances were not significantly different between recruitment variabilities (Bartlett's Test for homogeneity of variance: *Montastraea cavernosa*: test statistic = 2.204, p = 0.698, *M. annularis*: test statistic = 1.897, p = 0.755 and *Agaricia* spp.: test statistic = 1.019, p = 0.907). In order to determine why, the coefficient of variation for juvenile densities of *Montastraea annularis* were calculated for each recruitment probability distribution used, for each stage in their early life history (Figure 4.3). At the larval stage, variability was highest for the most skewed probability distribution used, as expected, and lowest for the Poisson recruitment probability distribution. But planktonic larval availability was not the life history stage with the highest variability; coefficients of variation rapidly increased during settlement until the end of the first year. All levels of temporal variability showed this trend. At the end of 4 years, there was little difference in the variability in density of *M. annularis* juveniles for the lowest three mean: variance ratios at recruitment, while the most negatively skewed recruitment distributions still had higher variability in juvenile density. So post-settlement processes had greater importance in structuring the modelled coral community than variability in larval supply.

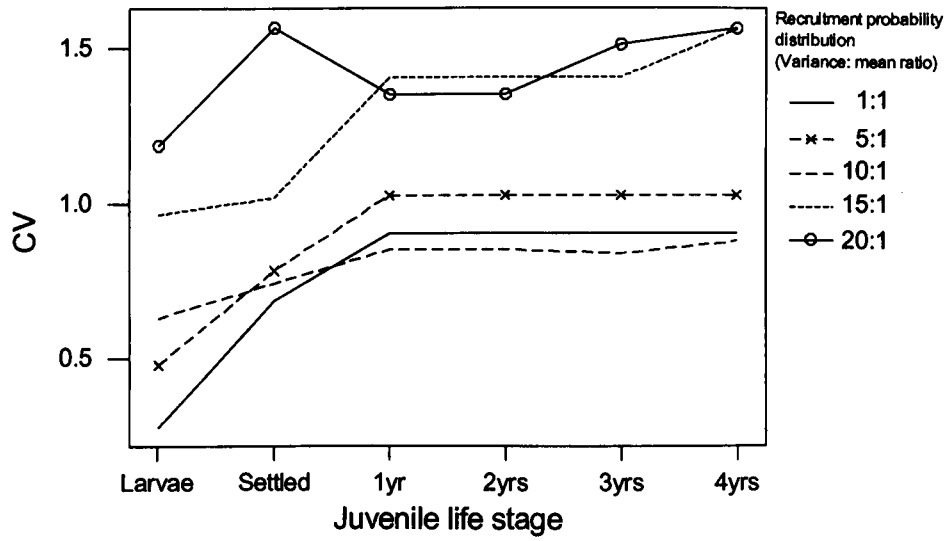


Figure 4.3 Effect of temporal variability in supply of recruits on density variability of *Montastraea annularis* juveniles during early life history stages. Temporal variability in recruitment given as negative binomial probability distributions with different ratios of variance: mean (each line), variability in juvenile density given as coefficient of variation (CV) within 10 replicate simulations.

4.4. Discussion

Testing the sensitivity of model outputs to a range of values for each life history variable not only tested the model for robustness to parameter changes, but also enabled better understanding of the relative importance of each process in structuring the coral community. The parameter whose changes most strongly affected coral composition was competitive ability. This is an interesting result as while the mechanisms of coral aggression are well described (Lang and Chornesky, 1990), their importance in structuring coral communities is not clear (Bradbury and Young, 1981; Connell, 1976; Sheppard, 1979). Frequencies of observed interactions can be low (Hughes, 1985) or extremely high (Sheppard, 1985b), and many additional factors can mediate outcomes (Bak et al., 1982). Methodological differences in addressing the importance of competitive interactions may in part explain such differences in opinion; specifically spatial scale (Sheppard, 1985b), and timing can influence results (repeated reversals in outcome can occur with broken by periods

where there is no evidence of interaction, Chornesky, 1989). On a physiological level, competition has been shown to influence rates of colony growth in one or both partners (Romano, 1990; Tanner, 1995) leading to measurable impairment in colony fitness (Tanner, 1997).

The high level of sensitivity of this model to changes in aggressive rank is consistent with Reichelt et al. (1985) who found that by including competition in a spatial simulation model, competitively dominant species swamped other benthic groups, concluding that either linear hierarchies of competitive ability are rare in coral reef benthic communities or are generally mediated by compensatory factors. However, an assumption of that model was that all benthic types (algae and corals) had equal rates of tissue turnover (growth and death rates), which is unlikely. Similarly, Karlson and Jackson (1981) found greatest model sensitivities for competition (influence of networks versus hierarchies) for sessile, clonal invertebrates, though in this case disturbance was completely omitted from the model. Cases against hierarchical (transitive) competition versus networks seem to originate from models with scant detail of disturbance processes.

While competitive rank has most influence on modelled community structure, greatest confidence is held in estimates obtained for that parameter, because these came from a single source (my own fieldwork) and do not contain potential error associated with derivation from different geographical regions, depths, reef types, or multiple observers. This strengthens confidence in model output. Similarly, while variations in rates of growth had the next greatest influence on model output, the range in growth rates from the literature is low, (e.g. *Porites astreoides* has a range of <2-fold, from 0.3 to 0.5 cm year^{-1} (Gladfelter et al., 1978; Highsmith et al., 1983 respectively). Thus, growth appears to be a very stable parameter as 5/10 species had low sensitivities when tested outside upper thresholds of their natural ranges, and high levels of confidence are held in growth rate estimates due to the consistency of measurement technique (depth of skeletal density bands).

Differential mortality and rates of recruitment influenced the model least, even when tested over large ranges. It is likely that measured recruitment rates contain error, for example estimates of *Porites astreoides* varies >8-fold from 16–133 settled larvae m^{-}

[2] (Rylaarsdam, 1983 and Tomascik, 1991, respectively). Rates of larval settlement also vary considerably over time and space (Connell et al., 1997; Hughes, 1985; Sammarco, 1991). However the single experiments yielding a snapshot view of this process are all that are available for use at the present time.

Each of the tested life history parameters influenced the dynamics of the modelled coral populations differently. Increasing growth rates increased mean colony size, and hence cover, while increasing recruitment rates, for the most part, had a negative effect on colony size. This was more pronounced in certain species, indicating a degree of density dependence e.g. *Agaricia* spp. and *Montastraea annularis,* suggesting that the overall amount of space is constrained by other factors, but population size structure within this space is a function of growth and recruitment. Other species did not show such a relationship, rather increasing in abundance, density and size with increases in recruitment or growth e.g. *Montastraea cavernosa* and *Eusmilia fastigiata.* Increased mortality decreased both colony sizes and numbers, but increased aggression influenced size of colonies rather than their density.

The inclusion of interactive reach into the model did not influence the community structure of the plot, but it did highlight the importance of this process to the dynamics of juvenile coral populations. These results are consistent with predictions that unoccupied space may not be ultimately available for recruitment if this open space is maintained by coral interactions (Sheppard, 1985b).

The temporal variability of recruits also did not influence community structure. Post-settlement processes had a stronger influence on the coral community than larval supply, and the community showed remarkable stability in this way. This is due to the high levels of post-settlement mortality. This is consistent with field observations (e.g. Bak and Engel, 1979 found that a third of all juveniles died during their first year, and Hughes, 1985 found that half died) and different rates of juvenile mortality have been found by species (Smith, 1992). This evidence implies that juvenile mortality is a highly important process that the model has captured it successfully. This also partly explains the robustness of model to changes in recruitment rates, and serves to increase confidence in model results.

Chapter 5. Comparison of model output to field data

5.1. Objectives

This section critically evaluates model output in terms of its success in predicting coral dynamics at community and population levels. To do this, coral population size structure, and colony abundance are evaluated.

Colony size structure on a reef is highly species specific, being the product of all coral life history processes (Meesters et al., 2001). The clonal nature of corals adds further complexity, as corals can undergo partial mortality shrinkage, fission and fusion. This means that coral age and size are progressively decoupled with age (Hughes, 1985). Thus if the model is able to predict colony size structures of coral populations from fundamental life history processes, it will simulate the dynamic processes acting on a population. For this reason, size structure is preferred to simple relative abundance.

The aims of this section were:

1. Assess the accuracy of model output by comparing population size structure to published observations.
2. Examine the influence of increasing levels of background disturbance. Sensitivity of the modelled coral community to disturbance, and the structure of communities at differing levels of background disturbance can yield insight into the strength of the model as a predictive tool, while individual responses of species help in understanding mechanisms structuring populations.

5.2. Methods

5.2.1. Model parameters and experimental design

Life history attributes for each coral species were identical to those used previously (Table 3.1 and differential mortality probabilities Table 3.3). Four simulations were run with increasing levels of background disturbance, by setting 0.05, 0.1, 0.15 and 0.2 of the modelled plot to bare substratum each year. Other disturbance parameters defining the powerlaw curve for determining background disturbance rates were: a = 1.5 (controlling the shape of the curve), R0 = 1 (minimum radius of disturbed patches) and R_{max} = 100 cm radius (maximum size of disturbed patches). These were kept constant throughout, with only the proportion of the plot affected by disturbance changing in each case. All simulations were run for 200 years. No additional model assumptions were required. Model output was taken as percent cover and number and size of colonies of each species at 200 years. 10 replicates were made at each disturbance level.

5.2.2. Analyses

Two sets of analyses were carried out: community analyses, where changes in the community composition were assessed, and, population analyses where changes to the colony size structure of individual species populations were quantified.

5.2.2.1. Community analyses

Percent cover data after 200 years were used to assess the influence of background disturbance rates. Communities were compared using multivariate analysis techniques, notably diversity indices (Equation 3.2) (calculated for each replicate and averaged across each disturbance level), and a Bray-Curtis similarity matrix constructed using all 10 replicates at each disturbance level. Differences at each disturbance level were analysed using a one-way analyses of similarity (ANOSIM). A multidimensional scaling (MDS) ordination was generated from the Bray-Curtis similarity matrix to quantify relative similarities between communities. A minimum stress value is given for the MDS ordination, indicating the strength of the two-

dimensional representation of multidimensional similarities; a low stress value signifies a good representation.

5.2.2.2. Population analyses

Population size structure was plotted for each species to assess the influence of increasing levels of background disturbance on the demography of species with contrasting life history strategies. All colonies from the 10 replicates were summed for broad sizes classes on a log scale (1-10, 11-100, 101-1000, 1001-10000 and >10000). The use of a log scale to model coral populations has been demonstrated to be a powerful tool for understanding their dynamics and species-specific responses to environmental processes (Bak and Meesters, 1998). For each species, the relative proportion of the total population in each size class was calculated (thus enabling comparison of populations with different sizes). Statistical comparisons were carried out using χ^2 Tests, using the total number of colonies (from 10 replicates) in each size class.

For certain species, the 95 percentile colony size (the threshold size below which 95% of the population falls) was used as a further descriptor of the effect of background disturbance. The 95 percentile colony size is more reliable than maximum colony size as a comparative measurement from the modelled plot as it is much less sensitive to small scale variability (Meesters et al., 2001).

Skewness, mean and median colony size for log transformed size distributions were also used to compare population structure and to define trends towards increasing or decreasing colony sizes under changing regimes of background disturbance. Skewness (asymmetry) is particularly informative, as it reflects the proportion of small versus large colonies within the population, a result of background disturbance processes and rates of growth and recruitment, which in turn has implications for population fecundity, rates of mortality and population viability.

To compare modelled coral size structures with those measured on real reefs, published data of colony sizes were examined. Where possible planar area was extracted, as this was directly comparable to model results, but in cases where colony sizes were given in other forms, transformation of model output was necessary. For

example, measurements of Meesters et al. (2001) were recorded as three-dimensional surface area and for the purpose of comparison, model output had to be transformed to the same scale. An assumption was made that massive species had hemispherical growth forms, thus multiplication by two (for each colony) yielded approximate three-dimensional surface area. Foliose growth forms could not be treated in this way, as the relationship between three-dimensional surface area and two-dimensional planar area is more complex, so these type of data were not compared, e.g. *Agaricia* spp. (RPM Bak pers. comm.). This derived secondary data was then sorted onto the same log scale as the modelled coral size structures.

5.2.2.3. Revising species attributes

Where some coral size structures were found to be markedly different from published field measurements, the model was further tested with different recruitment rates. Field recruitment data are highly variable and in the previous chapter it was demonstrated that recruitment rate can influence colony size structure in some coral species. For these simulations, the proportion of the plot affected by background disturbance was kept constant at 0.1, and three replicates of each parameter variation were made. Colony size output was taken after 200 years, as before.

In certain cases, a replicated goodness of fit analysis (Sokal and Rohlf, 1995) was employed to test for statistical differences between reported coral size structures and modelled size structures. This is similar in structure to a χ^2, but accommodates the replicated design of this study.

For *Montastraea annularis*, colony size frequency output was taken in two forms: 1) size of individual colonies and 2) size of genetic colonies (i.e. all the fragments from the same original or genetic individual). The reason for this was that *M. annularis* corals are long lived and frequently undergo fission, and when measured in the field, an obvious genetic individual with a common skeleton is likely to be considered a single colony even if the tissue is divided into distinct patches.

5.3. Results

5.3.1. Community structure

The modelled coral community structure shifted from one dominated by *Montastraea* spp. to a more diverse one with increasing levels of disturbance (Figure 5.1 a – d). At low levels of background disturbance (0.1), the modelled plot at 200 years was composed of around 47.5 ± 9.5% *Montastraea annularis* and 23.5 ± 7.8% *Montastraea cavernosa*, and while *Agaricia* spp. was present at abundances of 13.6 ± 7.5%, other species were rare (3.2 ± 2%) (mean ± 1 SD, n = 10). This community appears not to have reached a stable composition by 200 years, with trends of increasing abundance of *M. cavernosa* and consequent decreases in *M. annularis*, though all other species have consistent abundances from 100 years.

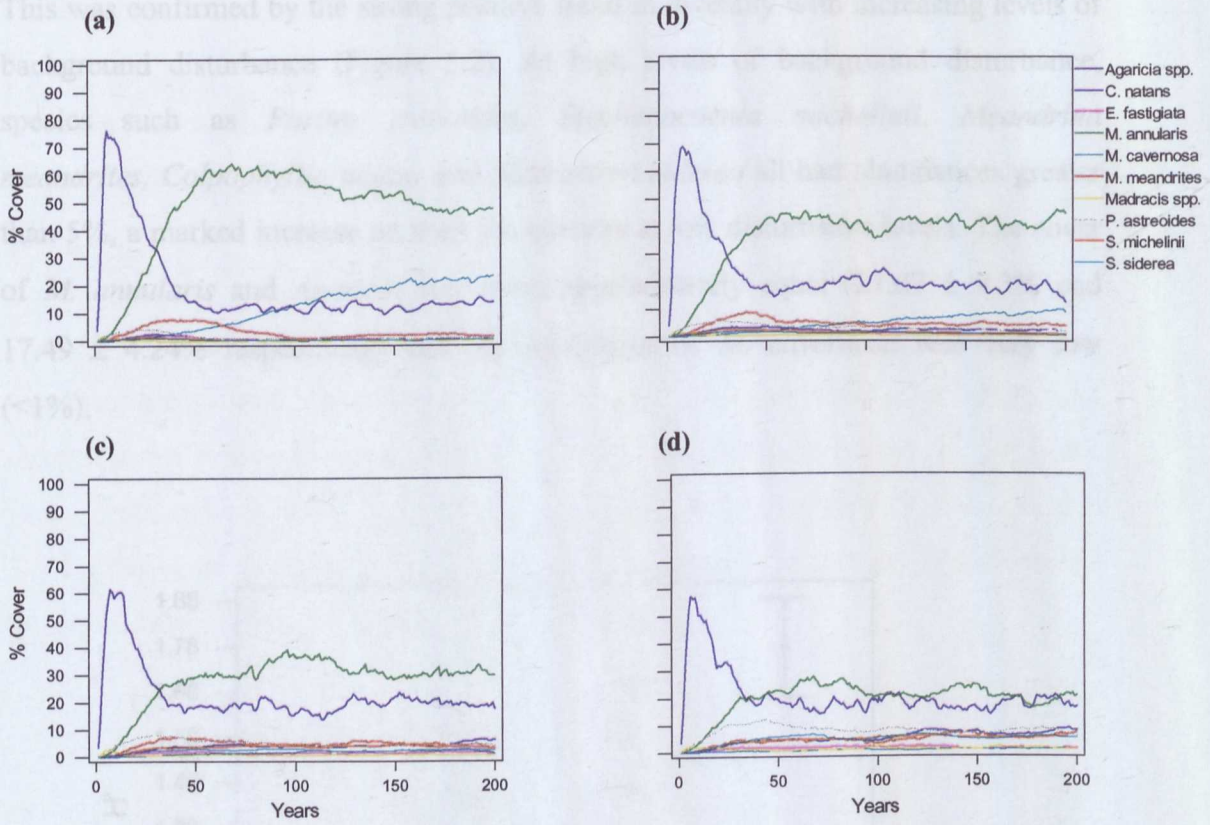


Figure 5.1 Community composition of the modelled plot run with background disturbance set at (a) 0.05, (b) 0.1, (c) 0.15 and (d) 0.2 (proportion of the plot affected each year). Each trace is mean of 10 replicates.

At intermediate levels of background disturbance, the community was dominated by *Montastraea annularis* and *Agaricia* spp. (Figure 5.1 b and c). These species were present at different relative proportions for background disturbance levels 0.1 and 0.15. *M. annularis* occupied 45.7 ± 12.4% at disturbance level 0.1, and 30.8 ± 9.63% at 0.15, while the opposite trend of increased abundance with increasing background disturbance was seen in *Agaricia* spp. (13.2 ± 4.6% and 18.7 ± 3.6% at disturbance levels 0.1 and 0.15 respectively). The abundance of *M. cavernosa* appeared to be increasing during the course of the simulation at disturbance level 0.1, suggesting that the community had not reached stability, similar to the trend seen at the lowest disturbance level. Groups with low abundances (<5%) at low disturbance levels (i.e. all except *Montastraea* spp. and *Agaricia* spp.) increased with increasing disturbance levels; 10.4 ±5.8% at 0.1 and 21.23 ±7.78% at 0.15 disturbance level), indicative of increasing levels of species diversity with disturbance.

This was confirmed by the strong positive trend in diversity with increasing levels of background disturbance (Figure 5.2). At high levels of background disturbance, species such as *Porites astreoides*, *Stephanocoenia michelinii*, *Meandrina meandrites, Colpophyllia natans* and *Siderastrea siderea* all had abundances greater than 5%, a marked increase on their abundances at low disturbance levels. The cover of *M. annularis* and *Agaricia* spp. were approximately equal (21.07 ± 9.3% and 17.49 ± 4.24% respectively) and the abundance of *M. cavernosa* was very low (<1%).

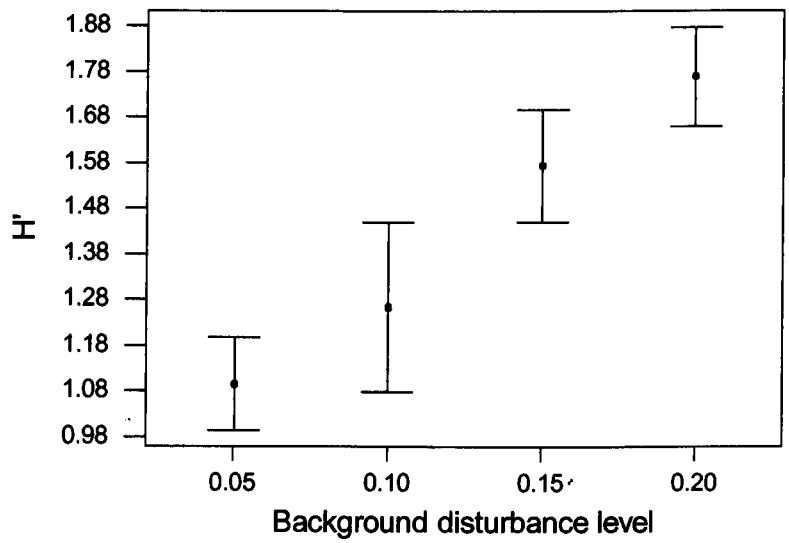


Figure 5.2 Effect of increasing levels of background disturbance on species diversity (H', Shannon and Weaver, 1948), (mean index ± 95% confidence intervals, n = 10)

Coral communities under different disturbance regimes reached stability (i.e. successional processes were complete) at varying times from initiation of the simulation. At low levels of background disturbance, stability was not reached. However, at higher levels of background disturbance, the community was stable after about 75 years.

Total coral cover decreased significantly with increasing levels of background disturbance (Table 5.1) (one-way ANOVA: $F = 8.49_{(df = 3)}$, $p < 0.001$). Differences in cover were only significant between 0.05 and 0.15, 0.05, 0.2 disturbance levels with

no differences detected between the 3 greatest disturbance levels (Tukey pairwise comparison).

Table 5.1 Total coral cover (%) at 200 years within the modelled plot with increasing levels of background disturbance (mean ± 1 SD, n = 10).

Proportion of the plot disturbed annually			
0.05	0.1	0.15	0.2
87.86 ± 3.36	78.25 ± 6.68	71.72 ± 11.40	72.82 ± 8.38

The MDS ordination of Bray-Curtis similarity matrix results indicates a strong linear sequence in coral community structure, with communities arranged from left to right across the ordination with increasing level of background disturbance). Furthermore, these communities were significantly different (one-way ANOSIM: $R = 0.806$, $p < 0.001$). Pair-wise comparisons confirm that communities at each level of disturbance are significantly different from all others (Table 5.2).

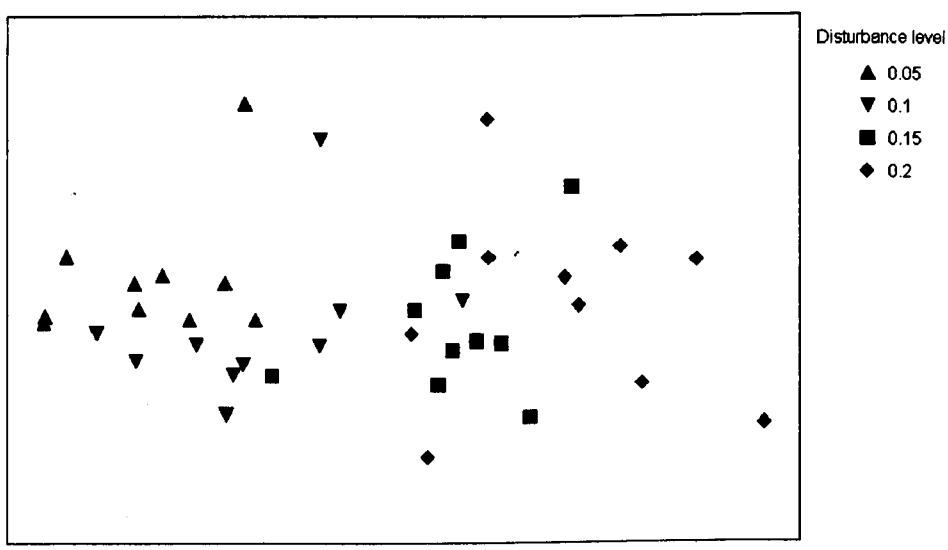


Figure 5.3 MDS ordination of Bray-Curtis similarity indices of species cover data indicating structural similarities of the modelled coral communities at 200 years under different levels of background disturbance, (n = 10 replicates). Minimum stress for the best 2-D configuration is 0.1.

Table 5.2 Significance of pair-wise comparisons from one-way ANOSIM comparing community structure at 200 years over increasing levels of background disturbance, as proportion of the plot affected each year (n = 10 replicates).

		0.05	0.1	0.15
0.1	R	0.782		
	p	<0.001*		
0.15	R	>0.999	0.694	
	p	<0.001*	0.002*	
0.2	R	>0.999	0.918	0.482
	p	<0.001*	<0.001*	<0.001*

* significant difference in community structure

5.3.2. Population size structure

Out of the ten species modelled, five compared well with published observations. Two species, (*Montastraea annularis* and *Agaricia* spp.), were initially markedly dissimilar in population size structure from observed populations, though after testing different rates of recruitment, highly comparable predictions were obtained. A further two coral species appeared to be modelled convincingly, though there were no field data available to verify this (*Madracis* spp. and *Stephanocoenia michelinii*). Finally, *Siderastrea siderea* population size structure was not comparable to real populations. For this species (and only this), modelled populations were consistently considerably smaller than observed populations. These species are examined in turn.

5.3.2.1. Coral species predicted accurately

Montastraea cavernosa

Background disturbance had strong influence on the size of the largest colonies of *Montastraea cavernosa.* Colonies decreased in maximum size with increasing levels of background disturbance, as did the variance around the 95 percentile size. Colonies grew to almost three orders of magnitude larger under low background disturbance regimes than they did when of .the proportion of the plot removed annually was 0.2 (

Figure 5.4). The lower background disturbance levels (0.05 and 0.1) allowed corals to reach sizes comparable with those measured by Soong (1993) and Meesters et al. (2001).

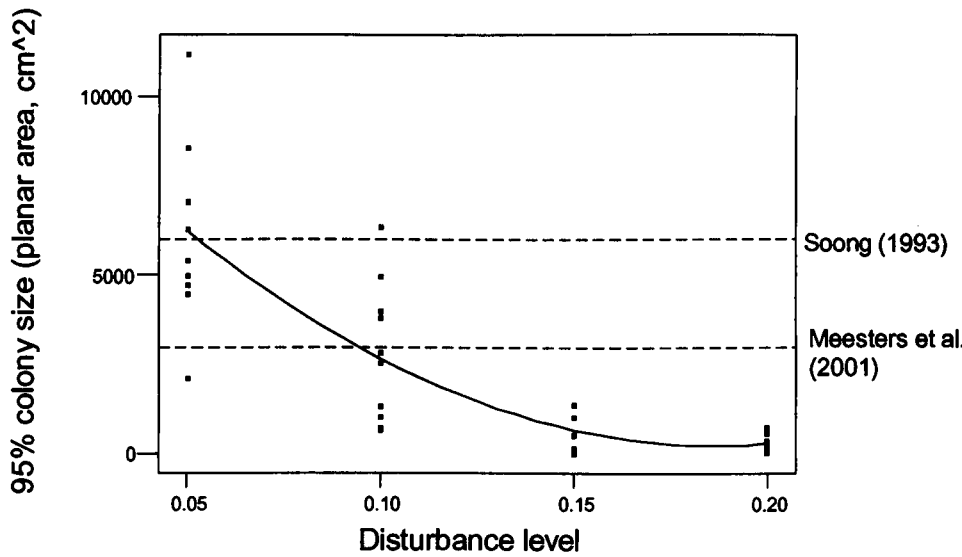


Figure 5.4 *Montastraea cavernosa.* 95 percentile colony size at 200 years with increasing levels of background disturbance (proportion of the plot affected each year), with field measurements from other workers indicated (n = 10 replicates).

This trend towards smaller colonies with increasing levels of disturbance was also reflected in the population size structure (Figure 5.5 a). At low levels of background disturbance, the modal size was 1001-10000 cm^2 three-dimensional surface area, comparing well to those measured in Curaçao (Meesters et al., 2001). The mode decreased by an order of magnitude with every increase of 0.05 in background disturbance level. Though levels of disturbance greater than 0.15 did not further affect the population size structure. This trend towards decreasing colony size with increasing background disturbance was significant (χ^2 test, all replicates from each disturbance level combined, $\chi^2 = 71.735_{(df=9)}$, $p < 0.001$).

The populations under low levels of background disturbance were heavily skewed towards larger size classes (Figure 5.5c), but at higher disturbance levels became normally distributed (Andersen-Darling test for normality on log-transformed colony sizes: $A^2 = 3.392$, $p < 0.001$, $A^2 = 2.458$, $p < 0.001$, $A^2 = 0.233$, $p = 0.818$ and $A^2 = 0.378$, $p = 0.399$ at background disturbance levels of 0.05, 0.1, 0.15 and 0.2 respectively). The number of colonies decreased with increasing background

disturbance and approximately halved between the lowest and highest disturbance levels.

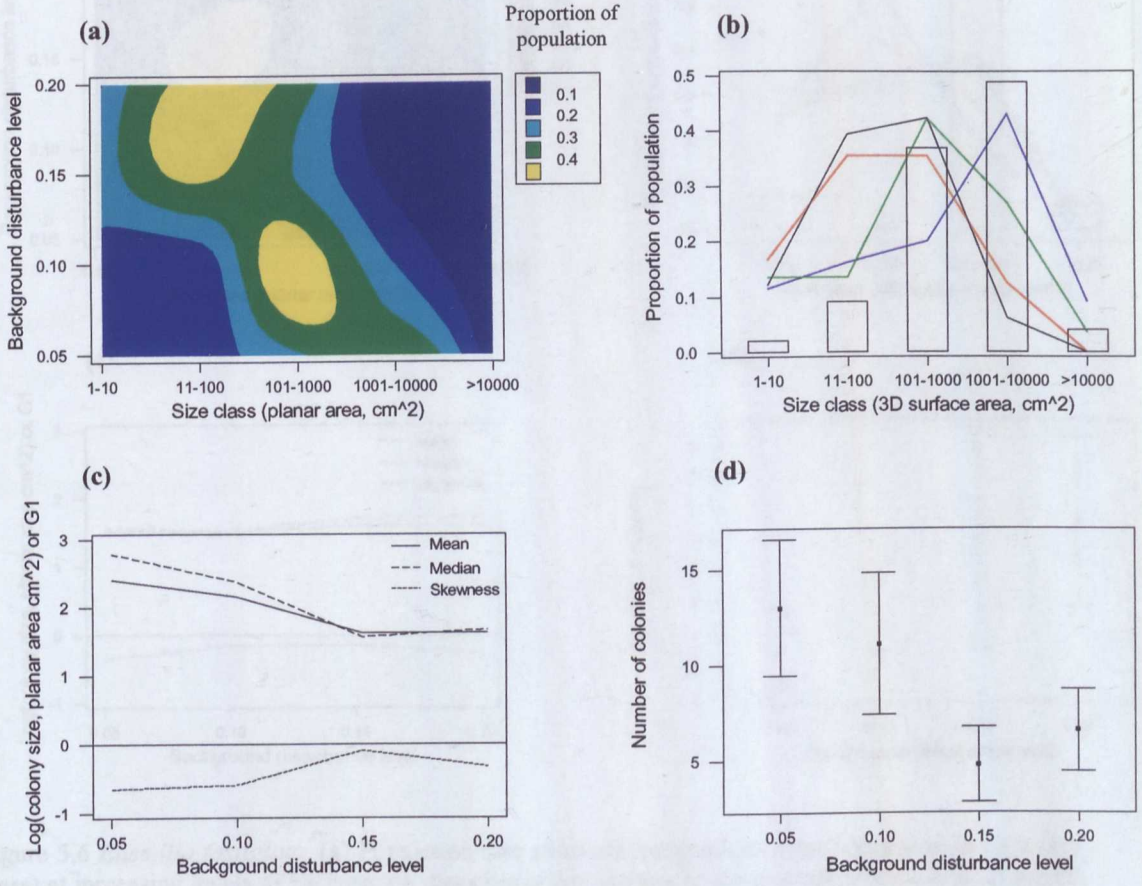


Figure 5.5 *Montastraea cavernosa.* (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels (transformed to three-dimensional surface area), 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations from Curaçao (combined for 2 sites) (Meesters et al., 2001). (c) Population statistics for increasing levels of background disturbance and (d) Number of colonies (mean 9 $m^2 \pm 95\%$ confidence intervals, n = 10).

Eusmilia fastigiata

The size structure of *Eusmilia fastigiata* populations was resistant to increasing background disturbance (Figure 5.6) (χ^2 test, on smallest three sizes classes using all replicates from each disturbance level combined $\chi^2 = 5.189_{(df=6)}$, $p = 0.520$).

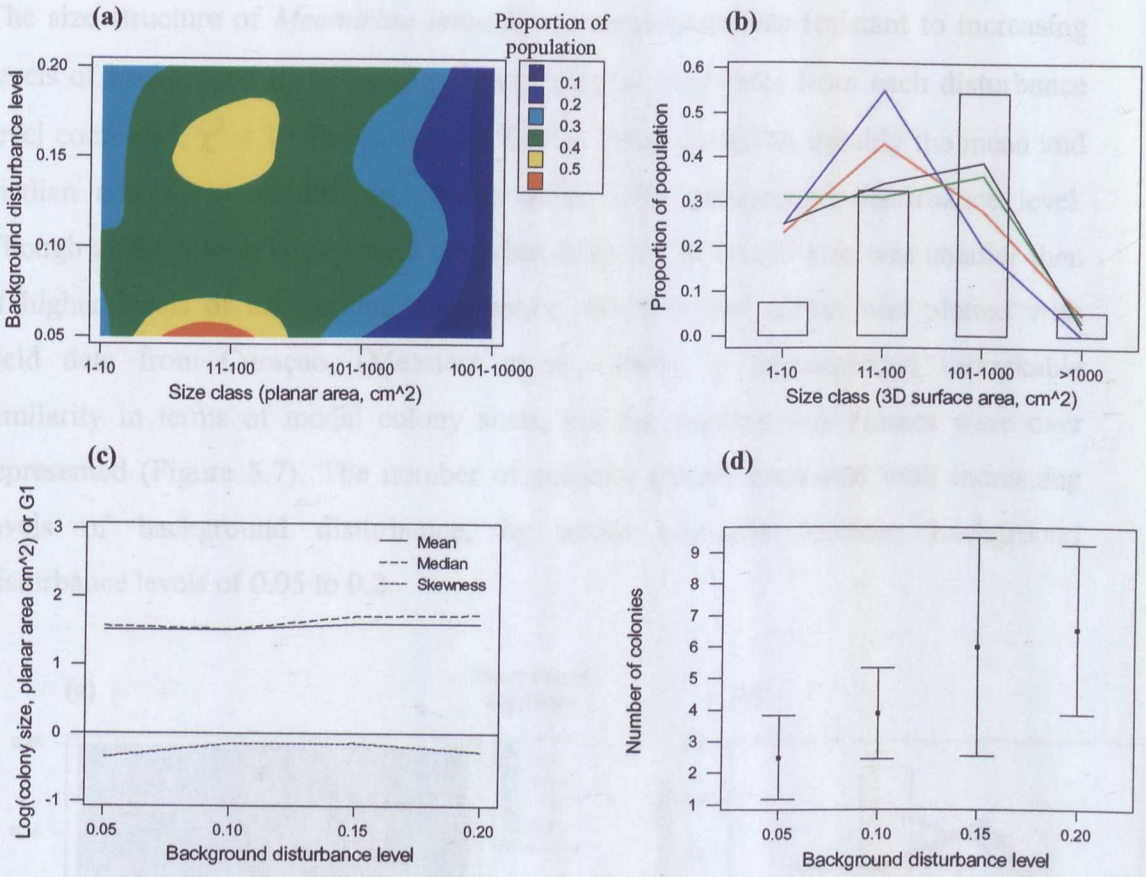


Figure 5.6 *Eusmilia fastigiata*. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels (transformed to three-dimensional surface area), 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations from Curaçao (combined for 2 sites) (Meesters et al., 2001). (c) Population statistics for increasing levels of background disturbance and (d) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

Modelled populations were comparable to those reported from Curaçao, (Meesters et al., 2001), in terms of the modal size, but in modelled populations the smallest size class was over represented. Background disturbance did not affect the mean, median or skewness of log normal frequency distribution. However, population size increased with disturbance level; at high disturbance levels (0.15 and 0.2), the population was much larger than at low disturbance levels (0.05 and 0.1).

Meandrina meandrites

The size structure of *Meandrina meandrites* populations was resistant to increasing levels of background disturbance (χ^2 test, using all replicates from each disturbance level combined, $\chi^2 = 10.904$ $_{(df = 9)}$, $p = 0.282$). Other statistics, notably the mean and median and skewness did not change either with background disturbance level. Though at the lowest background disturbance level, the modal size was smaller than at higher levels of background disturbance. When model output was plotted with field data from Curaçao, (Meesters et al., 2001), it demonstrated remarkable similarity in terms of modal colony sizes, but the smallest size classes were over represented (Figure 5.7). The number of colonies greatly increased with increasing levels of background disturbance, by about two-fold between background disturbance levels of 0.05 to 0.2.

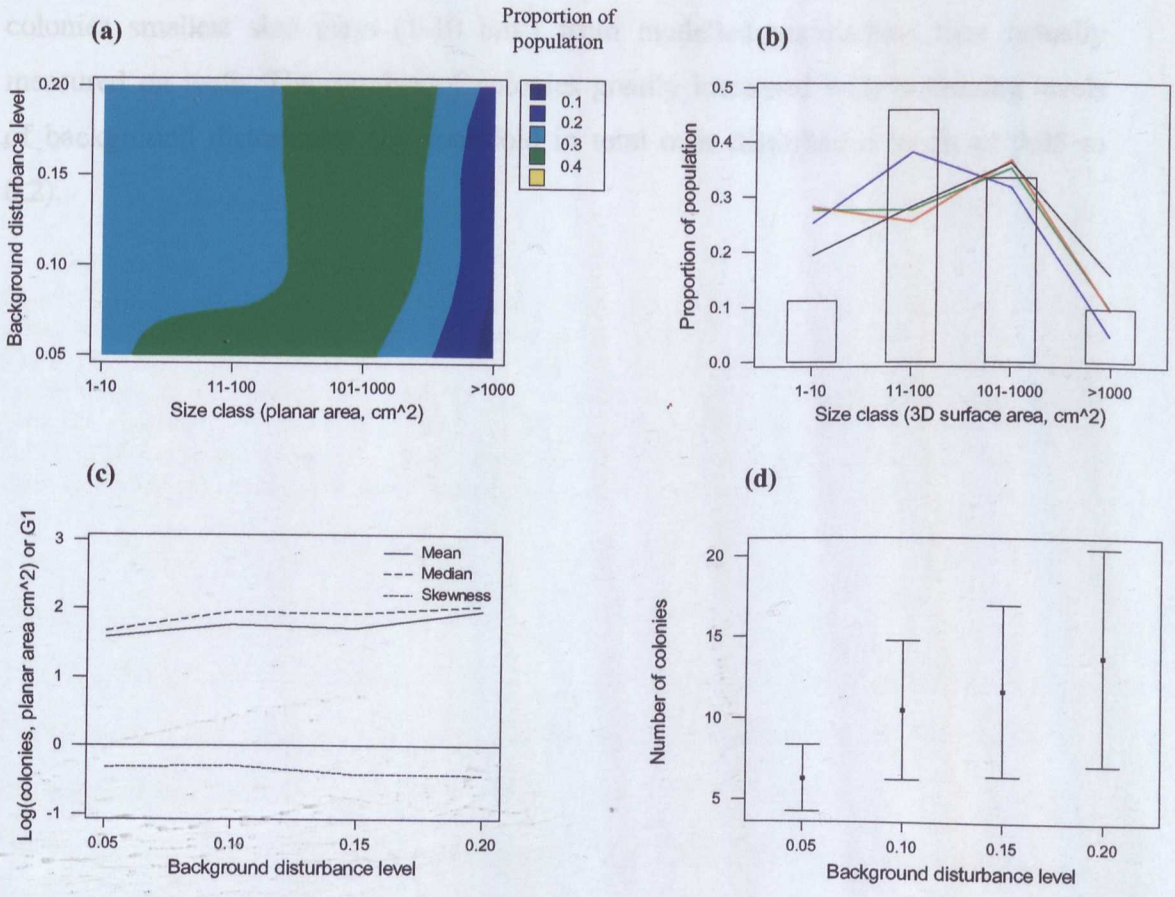


Figure 5.7 *Meandrina meandrites*. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels (transformed to three-dimensional surface area), 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations from Curaçao (combined for 2 sites) (Meesters et al., 2001). (c) Population statistics for increasing levels of background disturbance and (d) Number of colonies (mean 9 $m^2 \pm 95\%$ confidence intervals, n = 10).

Colpophyllia natans

The size structure of *Colpophyllia natans* was affected by background disturbance level (χ^2 test, using all replicates from each disturbance level combined, $\chi^2_{(df = 9)} = 17.660$, $p = 0.039$) (Figure 5.8). The modal colony size was 101-1000 cm^2 planar area for all levels of background disturbance but the number of small colonies decreased with increasing background disturbance, and the number of large colonies (1001-10000 cm^2) increased. This was reflected in the mean, median and skewness, the former two increasing with disturbance level, while the latter became more negative (i.e. the size structure became more skewed towards larger sizes). These results compared well to field observations by Meesters et al. (2001), especially at high levels of background disturbance, but like previous comparisons, there were more colonies smallest size class (1-10 cm^2) from modelled populations than actually measured on reefs. The number of colonies greatly increased with increasing levels of background disturbance (by four-fold in total over disturbance levels of 0.05 to 0.2).

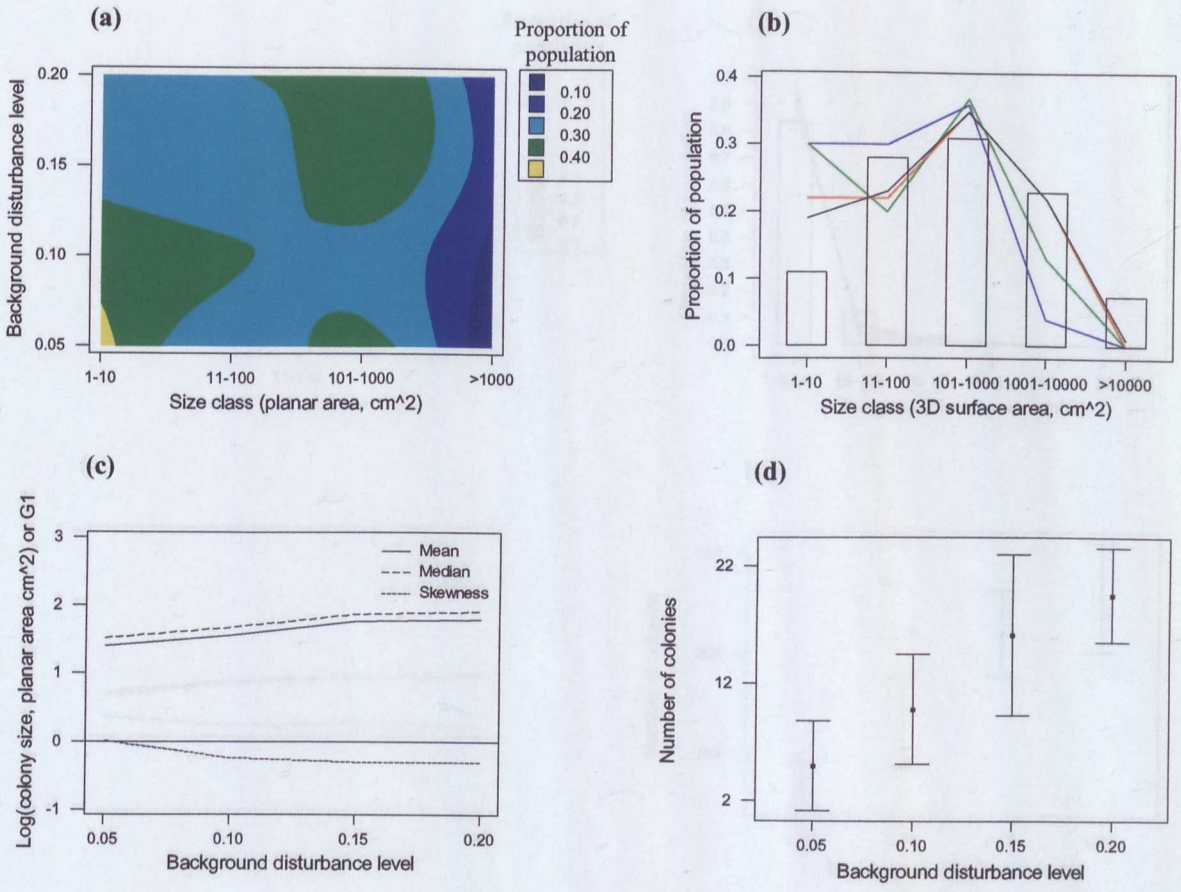


Figure 5.8 *Colpophyllia natans*. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels (transformed to three-dimensional surface area), 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations from Curaçao (combined for 2 sites) (Meesters et al., 2001). (c) Population statistics for increasing levels of background disturbance and (d) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

Porites astreoides

The size structure of *Porites astreoides* populations was influenced by rates of background disturbance, shifting from smaller to larger size classes (χ^2 test, using all replicates from each disturbance level combined, $\chi^2 = 116.251$, $_{(df = 6)}$, $p < 0.001$, Figure 5.9 a). These distributions compared well with field observations by Soong (1993). However the mean, median and skewness barely changed with increasing levels of background disturbance. There was a marked change in the number of colonies, which increased from 70.4 ± 31 to 256.1 ± 77 colonies per 9 m^2 yr^{-1}.

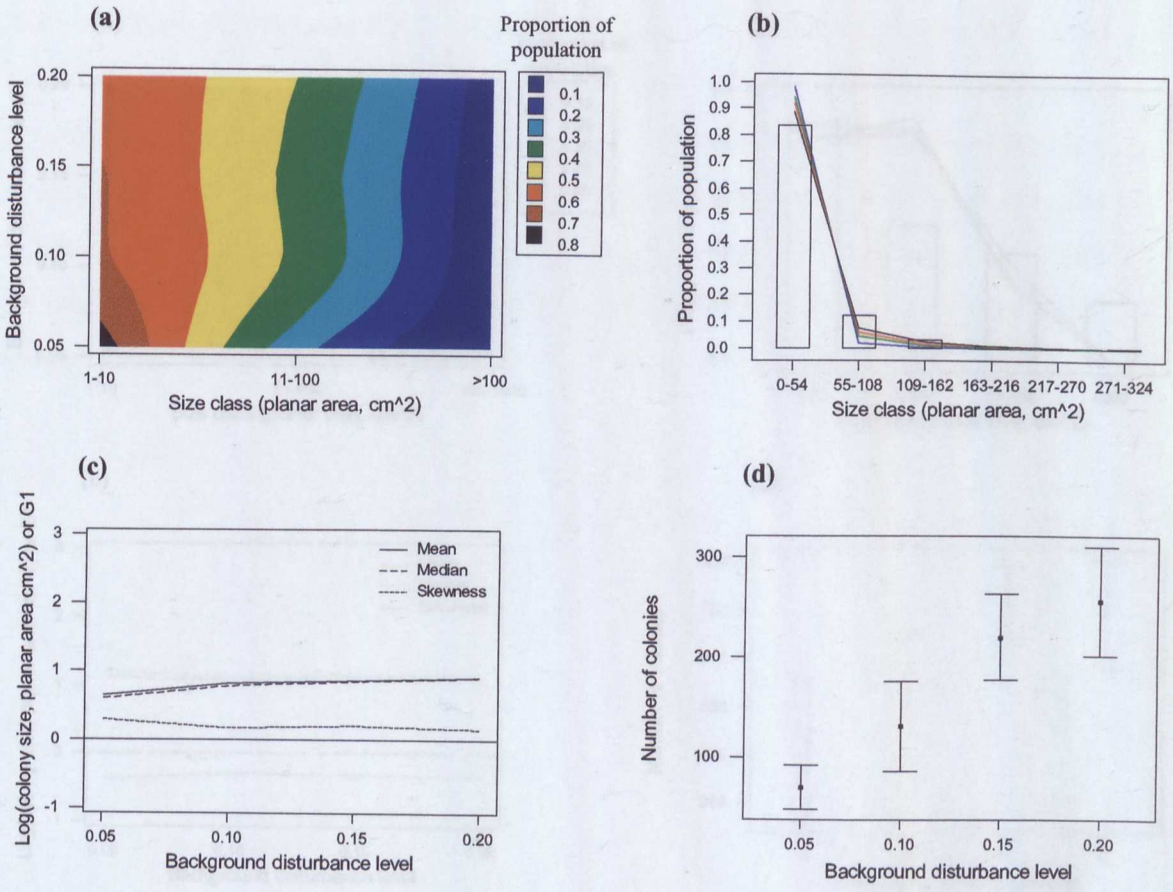


Figure 5.9 *Porites astreoides*. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels, 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations (Soong, 1993). (c) Population statistics for increasing levels of background disturbance and (d) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

5.3.2.2. Species which required further testing by varying recruitment rates

Agaricia spp.

The size structure of *Agaricia* spp. populations was resistant to increasing levels of background disturbance (χ^2 test, using all replicates from each disturbance level combined, $\chi^2 = 6.306$, $_{(df=6)}$, $p = 0.390$) (Figure 5.10 a and b).

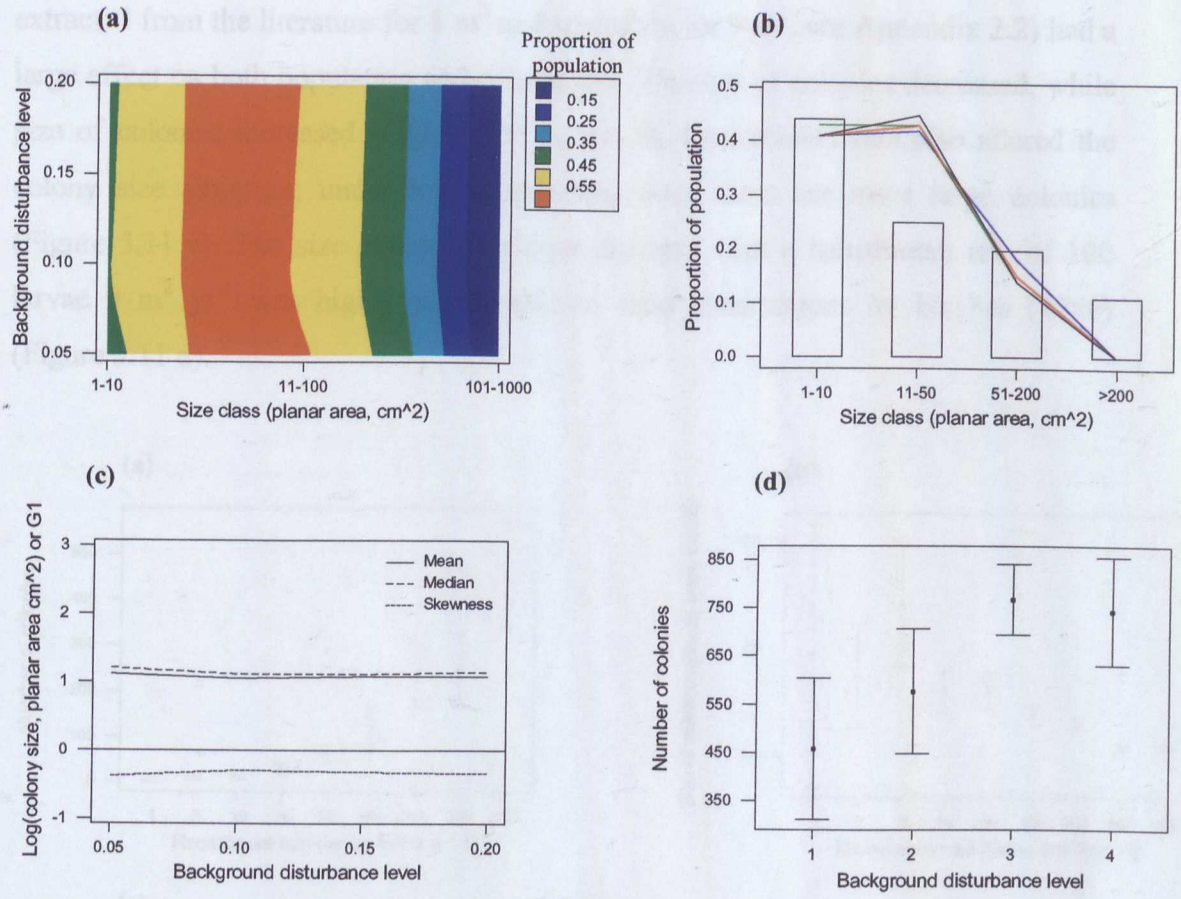


Figure 5.10 *Agaricia* spp. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels, 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations (Hughes, 1984). (c) Population statistics for increasing levels of background disturbance and (d) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

Modal colony size was small (1-10 cm^2 planar area). This consistency was also reflected in the mean and median colony sizes, and also the skewness of the log colony size distribution, which was slightly negatively skewed. Colony sizes, however, did not compare well to those measured by (Hughes, 1984) (Figure 5.10 b); the largest size class (>200 cm^2) was not represented by model output, while observations from real populations determined around 10% of colonies in this size class (Hughes, 1984). Also the modelled populations had more colonies in the second size class (11-50 cm^2) than observed populations. Population size, unlike colony size, was strongly influenced by the amount of background disturbance, with much larger populations at high levels of disturbance.

Decreasing recruitment rate from the initial value of 469 larvae 9 m^2 yr^{-1} (value extracted from the literature for 1 m^2 and scaled up for 9 m^2, see Appendix 2.2) had a large effect on both population and colony size. Number of colonies decreased, while size of colonies increased (Figure 5.11 a and b). Recruitment rate also altered the colony size structure; under low recruitment rates there are more large colonies (Figure 5.11 c). The size structure of *Agaricia* spp. with a recruitment rate of 100 larvae 9 m^2 yr^{-1} was highly comparable to field observations by Hughes (1985) (Figure 5.11 d).

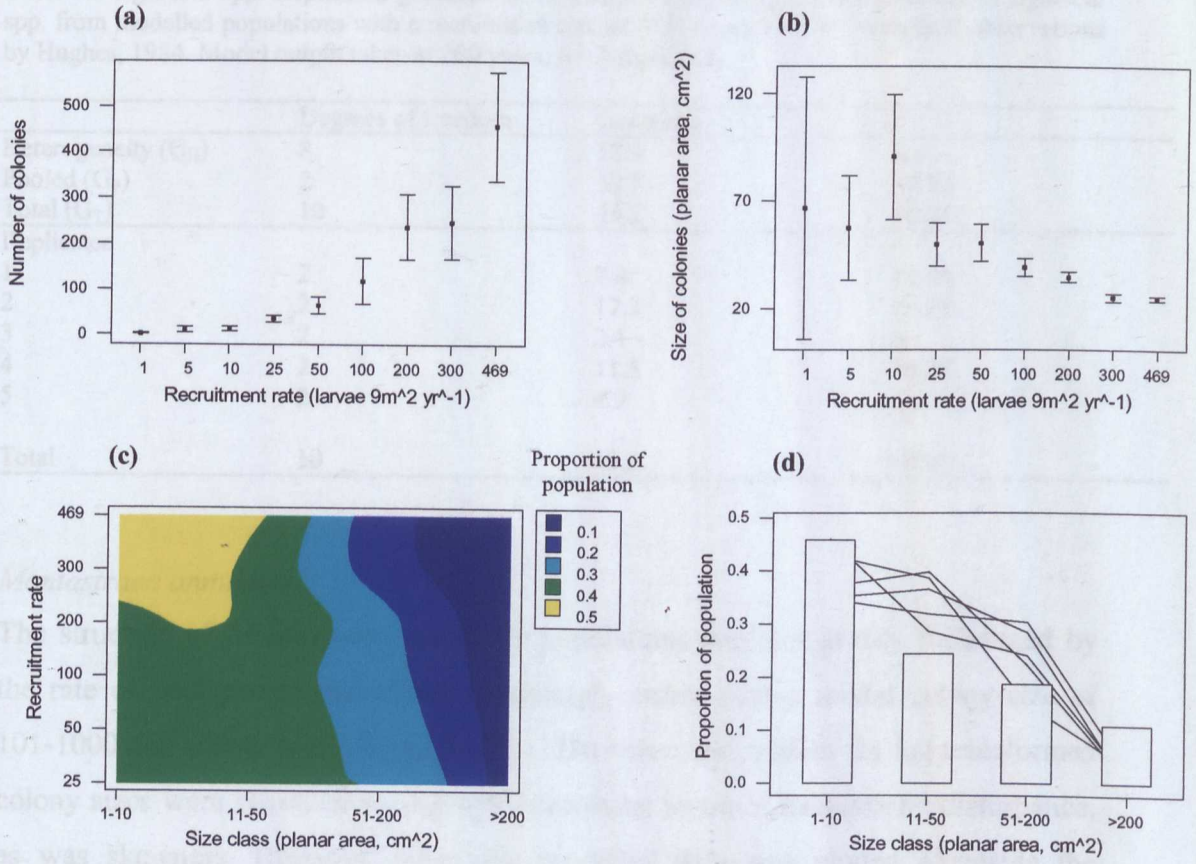


Figure 5.11 *Agaricia* spp. Effect of recruitment rate on (a) population size, (b) mean colony size (mean ± 95% confidence intervals, n = 5, model output taken at 200 years), (c) population size structure (recruitment rate given as larvae 9 m^2 yr^{-1}) and (d) comparison of modelled data with recruitment rate of 100 larvae 9 m^2 yr^{-1} (lines indicate results of five replicate simulations) with observed data (bars) (Hughes, 1984). All model output taken at 200 years.

Size structure of *Agaricia* spp. populations at a recruitment rate of 100 larvae 9 m^2 yr^{-1} were compared to observed data from Hughes (1984) using a replicated goodness of fit analysis (Table 5.3) (Sokal and Rohlf, 1995). To keep the number of

observations in each size class above five, the largest two size classes were combined. Initially, the size structure data from the five replicates were tested for heterogeneity (G_H, Table 5.3), and were found to be homogeneous. Subsequently, a pooled G-Test was carried out using Hughes' data as expected frequencies, and was found collectively to be significantly different (G_P, Table 5.3). The final part of the analysis was to test each trial individually against Hughes' data; two out of five replicates were not significantly different, indicating that in the model output compared to field results well in a proportion of the simulations.

Table 5.3 *Agaricia* spp. Replicated goodness of fit analysis comparing the size structure of *Agaricia* spp. from modelled populations with a recruitment rate of 100 larvae 9 m^2 yr^{-1} with field observations by Hughes, 1984. Model output taken at 200 years, n = 5 replicates.

	Degrees of freedom	G statistic	p
Heterogeneity (G_H)	8	12.5	n.s.
Pooled (G_P)	2	30.7	<0.05
Total (G_T)	10	43.2	<0.05
Replicates			
1	2	7.4	<0.05
2	2	17.3	<0.05
3	2	2.1	n.s.
4	2	11.5	<0.05
5	2	4.9	n.s.
Total	10	43.2	<0.05

Montastraea annularis

The structure of *Montastraea annularis* populations was not greatly influenced by the rate of background disturbance, seemingly stable with a modal colony size of 101-1000 cm^2 planar area (Figure 5.12 a). The mean and median for log transformed colony sizes were also unchanging with increasing levels of background disturbance, as was skewness. However, when the modelled data was plotted alongside the population structure of *M. annularis* measured from the field (Curaçao) (Meesters et al., 2001), it was clear that the modelled populations were substantially smaller in colony size (by 1 order of magnitude).

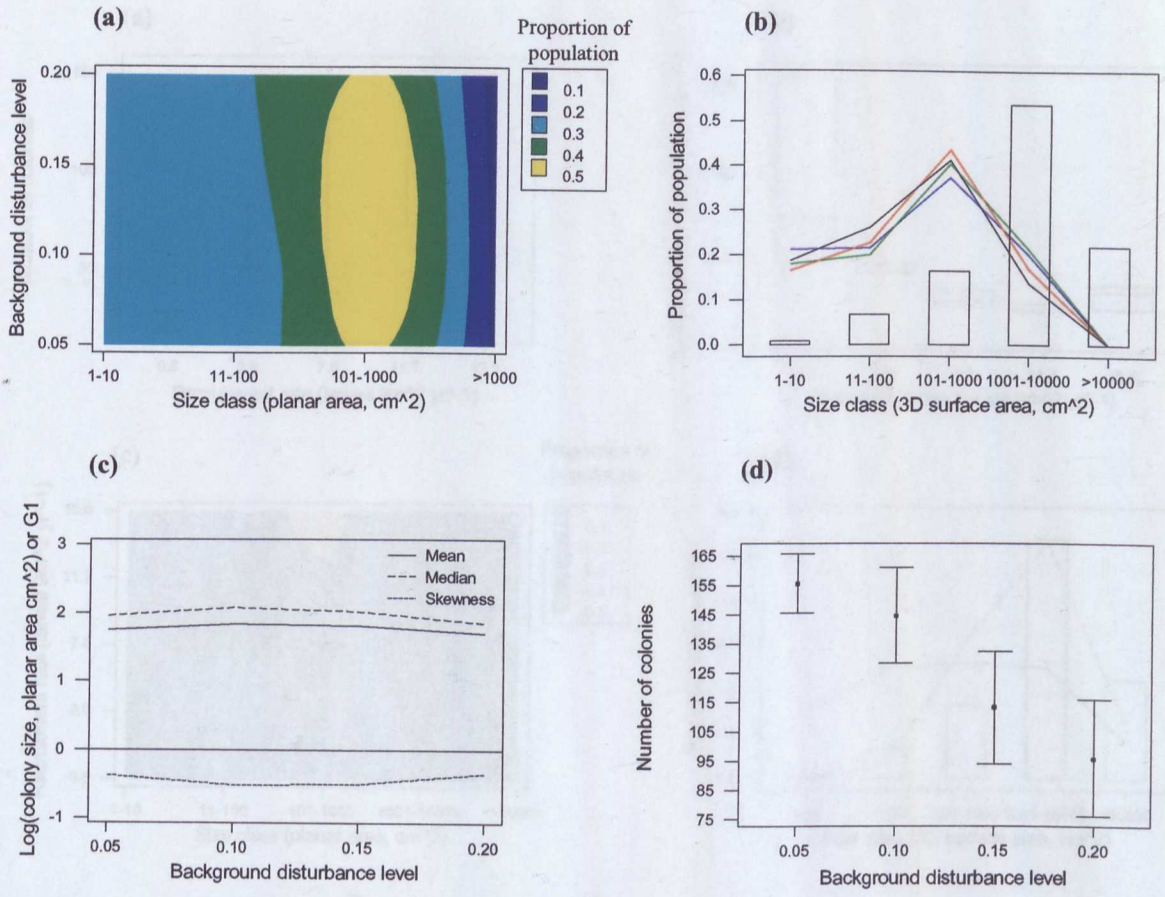


Figure 5.12 *Montastraea annularis*. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels (transformed to three-dimensional surface area), 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations from Curaçao (combined for 2 sites) (Meesters et al., 2001). (c) Population statistics over increasing levels of background disturbance and (d) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

Decreasing the modelled recruitment rate had a pronounced effect (Figure 5.13 a and b). Colonies were much larger under low recruitment rates, though there were fewer of them. When the two types of demographic measurement ('physically individual colonies' and 'genetic colonies' - see Methods) were compared with the field measurements of Meesters et al. (2001), the 'genetic' colony measurements were highly comparable.

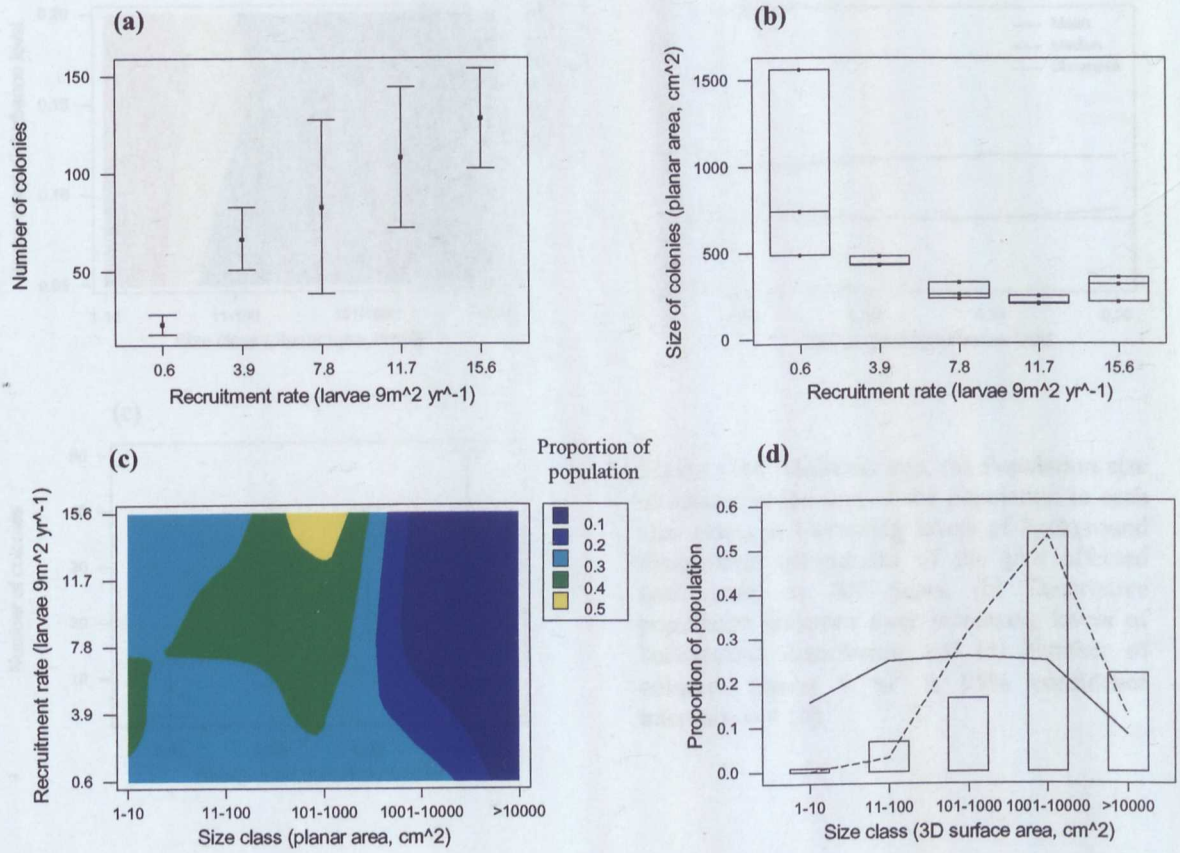


Figure 5.13 *Montastraea annularis.* Effect of recruitment rate on (a) population size, (b) mean colony size (mean ± 95% confidence intervals), (c) population size structure (replicates combined) and (d) comparison of modelled data (replicates combined) with recruitment rate of 0.6 larvae $9m^2$ yr^{-1} with observed data (bars) (Meesters et al., 2001), solid line shows all colonies measured as individuals, broken line shows colonies grouped as genetic individuals. All model output taken at 200 years, n = 3 replicates.

5.3.2.3. Species which could not be compared to field data

Madracis spp.

No field data was found with which to compare these modelled populations. The size structure of modelled *Madracis* spp. populations was not sensitive to changes in the rate of background disturbance (χ^2 test, using all replicates from each disturbance level combined: $\chi^2 = 10.718$, $_{(df = 6)}$, $p = 0.097$, Figure 5.14). Neither was there pronounced trends in log transformed mean or median colony size or skewness over increasing disturbance levels.

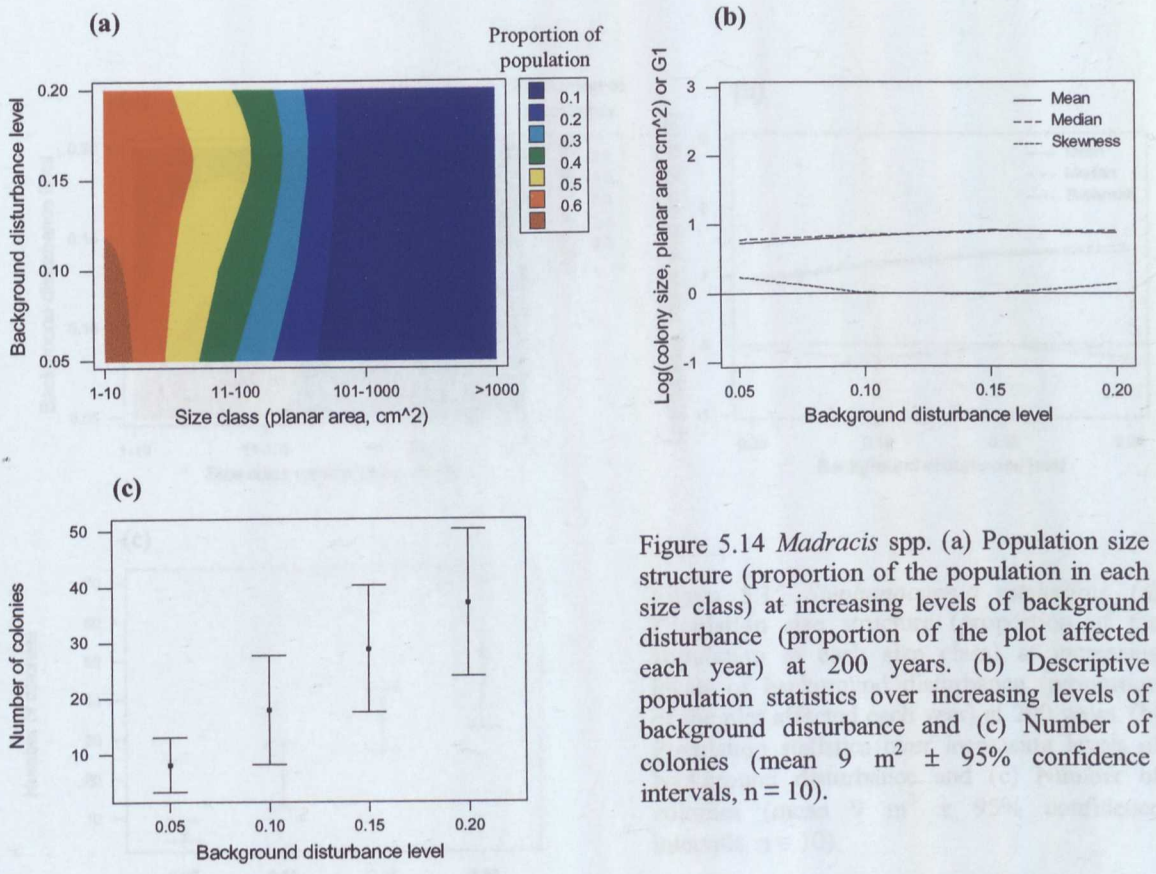


Figure 5.14 *Madracis* spp. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Descriptive population statistics over increasing levels of background disturbance and (c) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

Stephanocoenia michelinii

As with *Madracis* spp., no field measurements could be found in the literature with which to compare the predicted populations. Background disturbance rate had a significant influence on the size structure of *Stephanocoenia michelinii* populations (χ^2 test, using all replicates from each disturbance level combined: $\chi^2 = 51.145$, $(df = 6)$, $p<0.001$, Figure 5.15 a). At low levels of background disturbance, colonies were small (modal size of 1-10 cm^2), but increased in size with increasing levels of background disturbance (as seen in the log-transformed mean and median colony sizes), though the overall shape of populations remained relatively stable, (skewness, Figure 5.15 b). The number of colonies increased markedly with high levels of background disturbance (Figure 5.15 c).

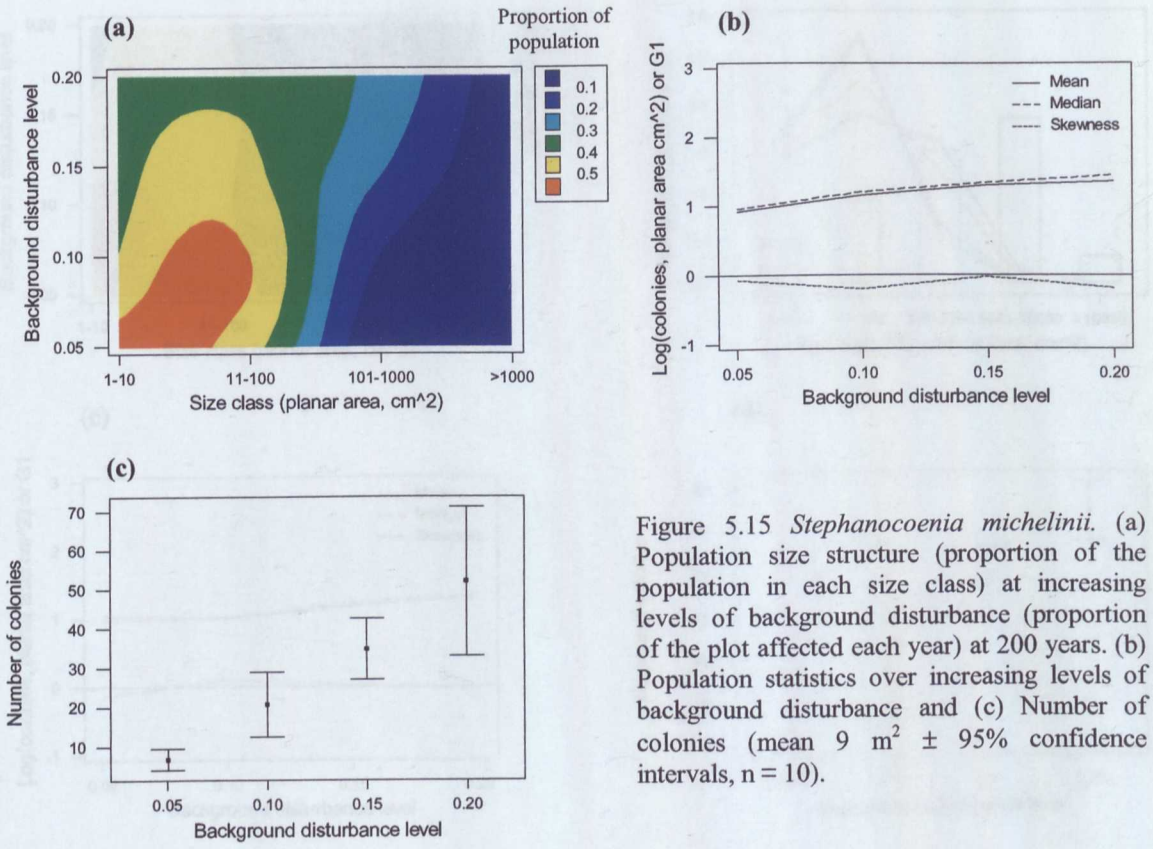


Figure 5.15 *Stephanocoenia michelinii.* (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Population statistics over increasing levels of background disturbance and (c) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

5.3.2.4. Species not predicted well by the model

Siderastrea siderea

Siderastrea siderea population size structure showed sensitivity to increasing background disturbance, with largest colony sizes under regimes of high disturbance (χ^2 test, using all replicates from each disturbance level combined: $\chi^2 = 40.41$, $(df = 6)$, $p<0.001$, Figure 5.16 a and b).

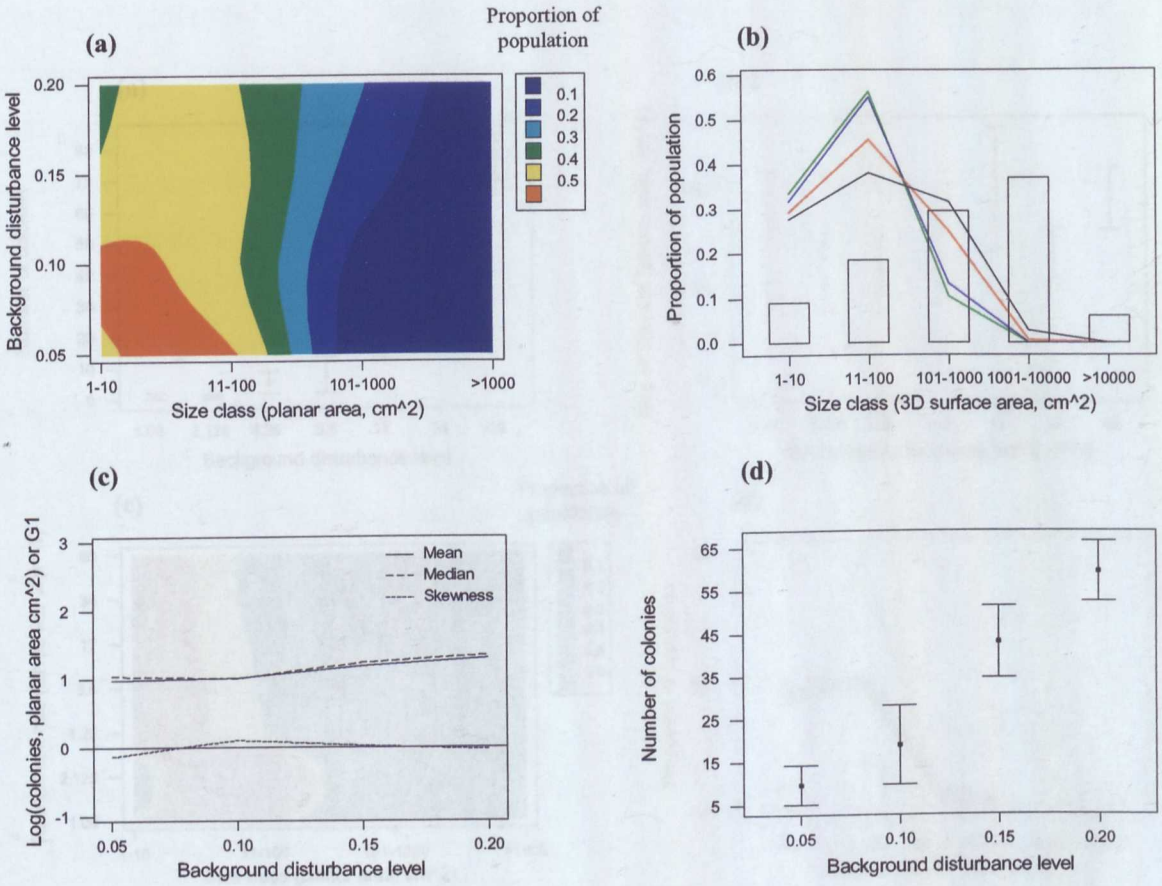


Figure 5.16 *Siderastrea siderea*. (a) Population size structure (proportion of the population in each size class) at increasing levels of background disturbance (proportion of the plot affected each year) at 200 years. (b) Comparison of modelled coral size structure to published field observations. Lines show model output at different disturbance levels (transformed to three-dimensional surface area), 0.05 – blue, 0.1 – green, 0.15 – red and 0.2 black, bars indicate field observations from Curaçao (combined for 2 sites) (Meesters et al., 2001). (c) Descriptive population statistics over increasing levels of background disturbance and (d) Number of colonies (mean 9 m^2 ± 95% confidence intervals, n = 10).

While the mean and median colony size of log transformed data increased with increasing disturbance, populations remained evenly structured; all were approximately log normal. The modelled populations differed markedly in their size structure from published observations. Modal colony size was 11-100 cm^2 for modelled populations, while observed populations had a modal size of 1001-10000 cm^2, two orders of magnitude greater. Size of *S. siderea* populations was also affected by the rate of background disturbance, with much larger populations occurring at high rates of disturbance (Figure 5.16 d).

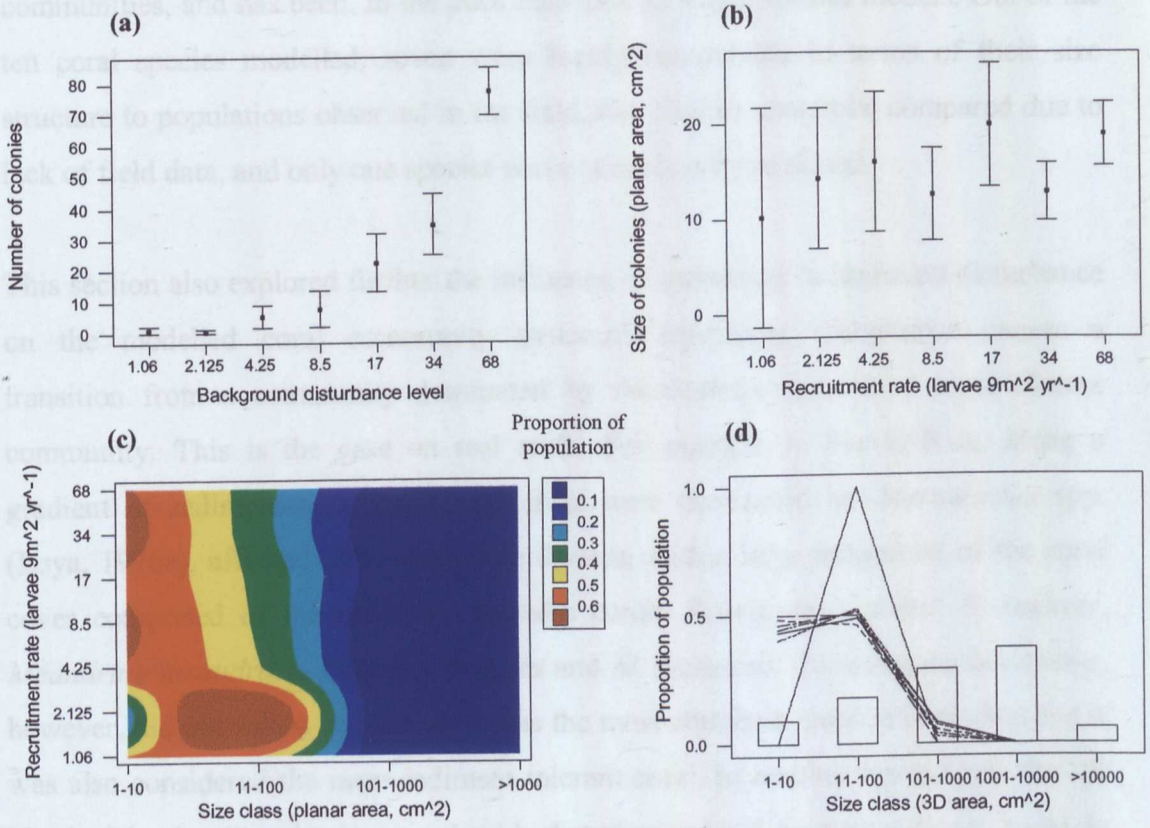


Figure 5.17 *Siderastrea siderea*. Effect of recruitment rate on (a) population size, (b) mean colony size (mean ± 95% confidence intervals), (c) population size structure (replicates combined) and (d) comparison of modelled data (replicates combined) at different recruitment rates with observed data (bars) (Meesters et al., 2001). All model output taken at 200 years, n = 5 replicates.

Recruitment rate had a strong influence on the number of *Siderastrea siderea* colonies, with many more colonies apparent at high recruitment rates (Figure 5.17). Unusually, The size of colonies was not sensitive to rate of recruitment, but variability around the mean size was larger at low recruitment rates (due to the low numbers of colonies). Thus adjusting the rate of recruitment did not render modelled populations more similar to those measured in the field, and modal colony size was consistently two orders of magnitude smaller than observed populations. Reasons for the models failure to accurately predict *S. michelinii* populations are discussed later.

5.4. Discussion

The model simulates well the complex dynamics of this coral community, and is able to predict demographic properties of communities to a high level of resolution. This

level of information is unprecedented for models predicting multi-species communities, and has been, in the past, restricted to single species models. Out of the ten coral species modelled, seven were highly comparable in terms of their size structure to populations observed in the field, two species cannot be compared due to lack of field data, and only one species was not accurately predicted.

This section also explored further the influence of increasing background disturbance on the modelled coral community structure. Increasing disturbance causes a transition from a community dominated by *Montastraea* spp. to a more diverse community. This is the case on real reefs. For example in Puerto Rico, along a gradient of sedimentation, unaffected areas were dominated by *Montastraea* spp. (Loya, 1976a), affected sites were more diverse, with a large proportion of the coral cover comprised of the normally sporadic corals *Siderastrea siderea*, *S. radians*, *Meandrina meandrites*, *Diploria strigosa* and *M. annularis*. *Montastraea cavernosa*, however, did not follow this trend; it was the most abundant coral at both sites, but it was also considered the most sediment tolerant coral. In another report from the US Virgin Islands, diversity increased with disturbance level (sedimentation), *Agaricia agaricites*, *Siderastrea radians* and *Porites porites* were the most abundant corals in a heavily sedimented locality (Rogers, 1990). Other evidence of disturbance structuring communities, and the sensitivity of *M. annularis* populations to high background disturbance levels comes from studies of zonation patterns from Caribbean reefs, where *M. annularis* dominated zones were determined to be strongly controlled by wave exposure (i.e. these zones occur shallower in low energy environments) (Geister, 1977).

Coral cover in the modelled plot was least at high disturbance levels. This inverse relationship between disturbance level and coral cover has also been predicted using other modelling techniques under different regimes of wave exposure (Graus and Macintyre, 1989). In fact from all of the physical parameters that influenced the structure of coral communities explored in that study, wave exposure was the second most influential (after depth). Thus not only does the modelled coral community display sensitivity to levels of background disturbance, but community transitions also simulate those seen along natural disturbance gradients (from varied causal agents).

The modelled plot had comparatively high coral cover, ranging from 72.82 ± 8.38% to 87.86 ± 3.36% over background disturbance levels of 0.05 to 0.2. Documented total coral cover, while spatially and temporally variable, is generally around half this value; Curaçao 34% (Bak and Luckhurst, 1980), Bermuda 16% and 36% (Dodge et al., 1982; Fricke and Meischner, 1985 respectively), Florida 25% (Porter and Meier, 1992), Jamaica 50% and 32% (Goreau, 1959; Liddell and Ohlhorst, 1987 respectively). The most obvious reason for this disparity is related to one of the primary specifications of the model: the plot is homogeneous rock, i.e. all space within the plot was equally suitable for coral growth. This is rarely the case on coral reefs where a number of other physical or biological components can cover significant proportions of primary space. The three most important of these elements are:

1. Rubble, sand or fine sediments, which render areas unavailable for colonisation and growth by corals.
2. Algae, which can occupy considerable and variable amounts of space on coral reefs. Up to this point in the study, algae are not modelled (though are included from Chapter 6).
3. Other attached fauna. As explained earlier, the model includes coral-occupied space over the entire plot for computational efficiency.

Thus overall coral cover is higher than levels observed on real reefs. However, the relative cover of each species is highly comparable. The total coral cover of the modelled plot could be corrected by introducing spatial heterogeneity, with areas where corals are unable to inhabit, but as no more information would be gained by such a technique (in fact, around half the plot would be lost in this way), this was not attempted. In terms of the level of information yielded by each type of data, cover is less informative than the population size structure of coral species, as noted earlier.

Size structures of modelled populations showed remarkable similarity to observed populations from various Caribbean reefs for five species. These species were *M. cavernosa, P. astreoides, E. fastigiata, M. meandrites, C. natans*. With respect to the smallest size class (1-10 cm^2 planar area), modelled populations invariably had more small colonies. Two hypotheses could explain this: 1) small corals are frequently

underestimated during field censuses due to their size and preference for cryptic habitats (and also identification of small sized individuals can be more difficult), or 2) mortality rates for the earliest post-settlement stage were underestimated in the model. Juvenile corals are more vulnerable to total colony mortality than larger ones (Bak and Engel, 1979; Hughes, 1985), and while this was not explicitly simulated within the coral community model, rates of total colony mortality were demonstrated earlier to be dependant on the size of disturbed patches, which was set at the threshold level between total and partial colony mortality (i.e. mean disturbed patch size was set at the maximum size at which coral is likely to suffer total colony mortality). Thus modelled corals had a high rate of total colony mortality up to a preset size, above which the chances of total colony mortality decreased, and partial mortality increased. (See Chapter 3, Section 3.3.2).

Seven out of ten modelled coral populations were negatively skewed, the exceptions being *Porites astreoides, Madracis* spp. and *Siderastrea siderea.* Negative skewness indicates that colony size distributions have fewer smaller colonies relative to larger ones. This is highly comparable with distributions measured by Meesters et al. (2001), who determined 48 out of 52 populations measured to be negatively skewed. That study also found a positive relationship between mean colony size and the degree of negative skewness. It is interesting to note that species in this study that were not negatively skewed were generally those with the smallest colonies.

Population size structure of some coral species was sensitive to increased rates of background disturbance. The latter both forced populations towards smaller or larger colony size classes, depending on the species. Populations of *Montastraea annularis* and *M. cavernosa* both became less skewed (i.e. moved towards log normal populations structure, by either gaining more smaller sized colonies or loosing larger ones) with increasing levels of background disturbance. This is similar to the trend in *Montastraea annularis* populations from control and degraded reefs in Curaçao, though *M. cavernosa* was not found to change between sites (Meesters et al., 2001). Species that grew larger colonies under high background disturbance included *Colpophyllia natans, Porites astreoides* and *Siderastrea siderea.* The following species did not change in size: *Meandrina meandrites, Eusmilia fastigiata, Madracis* spp, *Agaricia* spp. Although Meesters et al. (2001) also found some coral species to

be relatively stable in terms of their mean colony size across sites, the corals were from different species to those found here, notably *Dichocoenia stokesii, Montastraea cavernosa* and *M. faveolata* (which is included in the *M. annularis* species complex in this study).

Initially *Agaricia* spp. and *Montastraea annularis* population dynamics were not captured convincingly by the model, but after adjusting their recruitment rates, their simulated behaviour compared with field measurements. In both cases, initial estimates of recruitment rate were too high, and their adjustment downwards here was to a level still within the range of field observations. Also *Agaricia* spp. has extremely high post-settlement mortality rates (Hughes and Jackson, 1985). It is possible that this high post-settlement mortality was not entirely accounted for in the model and reduction of recruitment rate compensated for this. The case of *Montastraea annularis* is more readily explained. A spurious observation of 36 recruits m^2, or 11% of the total recruitment complement, pushed up the average recruitment value of *M. annularis* from 0.3 to 15.6 recruits 9 m^2 yr^{-1} (Tomascik, 1991) (Appendix 2.2). This anomalous result either was made during a 'mast' year with unusually high reproductive output and consequent recruitment success (Hughes and Tanner, 2000) or juvenile colonies were misidentified (*M. annularis* is a Faviid and juveniles look similar to *Favia fragum*, and may actually have been recruits of this highly fecund brooder). Regardless of which factor actually caused the anomalous observation, recruitment rate with this measurement removed is 0.3 recruits per 9 m^2 yr^{-1}, similar to the derived value of 0.6 recruits per 9 m^2 yr^{-1}.

Only modelled *Siderastrea siderea* populations were very different in structure from observed populations. There is likely to be some discrepancy in the input life history attributes for this species. *S. siderea* has low rates of recruitment and growth, is susceptible to mortality, and has minimal competence during spatial competition, so the small colony sizes generated by the model are not entirely surprising. The question remains, how does this species persist in such large numbers of large colonies on reefs? One possible solution may relate to substrate heterogeneity, and utilisation of spatial refuges. A congener, *S. radians*, is extremely tolerant of sandy/silty conditions, and can even survive unattached, and roll freely across sandy lagoonal areas by surge (Humann, 2001). This would suggest a high resource

investment in sediment removal and tissue regeneration mechanisms, possibly with trade-offs in reproduction and growth. *S. siderea* may use a similar strategy, and survive in marginal areas of the reef, for example adjacent to areas of unconsolidated substratum. To date there is no evidence available to suggest that this is the case, but this hypothesis may be worth further consideration.

The strong resemblance of modelled to observed population structures demonstrates that the powerlaw model works well in assigning sizes of disturbed patches, and that the other disturbance parameters (a, R_{max} and R0) used in this study were accurate at generating realistic levels of total colony mortality and partial mortality. Thus assumptions on disturbance patterns in time and space as defined in Chapter 3 appear to be realistic. From this section we can conclude that coral population structure, for most species, is extremely predictable, and can be achieved using rates of recruitment and growth from wide ranging sources, in conjunction with a powerlaw model to determine rates of mortality.

There are many advantages in using this system over single species, size-structured transition models to predict coral populations (Done, 1987; Done, 1988; Fong and Glynn, 1998; Hughes, 1984; Hughes and Tanner, 2000). Firstly, it can be utilised to investigate mechanisms operating simultaneously at community and population levels, whereas other models are restricted to single species and do not take into account dynamic interactions between species. Secondly, spatial dynamics, an intrinsic property of coral reefs, are accounted for. The treatment of coral colonies as modular units is intuitive, and permits capturing of complex life history processes such as fission, fusion and partial mortality, and also tracking of genetic individuals that have multiple ramets. On a practical level, markedly less information is needed to successfully model coral populations, with just five key parameters per species, compared to the enormous number of variables needed to construct a transition matrix model (e.g. each size class requires probabilities of colonies moving into it from smaller classes and out of it to larger classes (via growth), colonies moving to smaller classes (partial mortality) and a mortality rate (colony death) as well as the proportion of colonies remaining in it, and recruitment rates), all of which require years of monitoring populations to obtain reliable estimates. Finally, model output can be taken in the form of colony sizes on a continuous scale that is amenable to

statistical analysis of population characteristics, which cannot be computed with discrete size-classified data.

Chapter 6. Recovery following the impact of a single warming event and addition of algae

6.1. Objectives

The impact of a single disturbance event on a Caribbean coral community is investigated. The type of disturbance applied was a warming episode, the causal agent of much recent coral mortality. The overall objective of this chapter is to simulate the effect of a single warming event and investigate impacts on the modelled community, and quantify the immediate community response and subsequent recovery. The next chapter builds on the work undertaken in this one and simulates repeated warming events such as might be expected in the coming century.

Algae were included during this section, due to their role during reef recovery (Diaz-Pulido and McCook, 2002; McClanahan et al., 2001b). Rates of bleaching and thermally induced mortality were assigned to corals using reports of recent warming events. These were then applied to the modelled coral community, and impacts at varying intensities of warming were assessed. The rate and pattern of community recovery were examined.

Effects of warming events were chosen for a number of reasons; bleaching as a response to sea warming has been heavily researched in the last decade, and physiological mechanisms are largely understood (Brown, 1997; Hoegh-Guldberg, 1999). Also there is a wealth of ecological information on the immediate impacts of warming at varying intensities, in reports from wide ranging locations (Williams and Bunkley-Williams, 1988). Warming events are discrete and temporally restricted, thus can be considered an acute 'pulse' type disturbance (*sensu* Bender et al., 1984), a convenient single perturbation from which subsequent system response can be assessed within the framework of the modelled coral community. By contrast, more direct anthropogenically-generated disturbances such as pollution, increased run-off,

sedimentation and nutrification are usually chronic disturbances, inflicted over long time periods and are more likely to result in a direct and permanent change to the environment (i.e. altering current flow rates, reducing light penetration through the water column) (Dubinsky and Stambler, 1996; Pearson, 1981). Disturbances of these types are less tractable to the current model due their tendency to change the environment. Also the large amounts of information needed to base assumptions and parameters are simply not available. Most importantly, this is a highly topical area to investigate in the wake of repeated and damaging warming episodes recently (Wilkinson and Hodgson, 1999). Specific aims were to:

1. Integrate algae into the model. The interaction between corals and algae changes during warming events, and corals may be less able to compete spatially. Algae may occupy more space during warming events (Diaz-Pulido and McCook, 2002; McCook, 1999).

2. Investigate the influence of algal growth rate on the coral community response to warming events. The rationale behind this was two-fold: partly to assess whether this is a factor which the modelled community is sensitive to, and to determine whether reefs with high algal abundances are likely to have impaired coral recovery rates.

3. Examine the effect of different disturbance intensities on the coral community. The extent of damage to corals is one factor generally accepted to influence the rate of recovery (Pearson, 1981). Little is known of the pattern of community recovery following warming events or the factors that influence them, mostly due to the short period over which many reefs have been monitored.

4. Assess the influence of reef connectivity on the recovery processes following warming events. The degree to which a reef is recolonised by recruits produced by its own resident corals (as opposed to imported recruits from other reefs) may influence reef recovery, especially if the local population is rendered non-fecund by warming events.

6.2. Methods

6.2.1. Assumptions

The inclusion of algae presents difficulties because of the considerable structural and taxonomic diversity of algae present on Caribbean reefs and their differing interactions with corals (Aronson and Precht, 2000; de Ruyter van Steveninck, 1987; McClanahan et al., 2001a; Potts, 1977; Sammarco, 1980). However, algae may have a significant role in recovery processes of coral communities following bleaching (Diaz-Pulido and McCook, 2002), especially in the Caribbean (Hughes, 1994). Specific assumptions were:

1. 'Algae' includes all benthic algae (filamentous, turfing, blue-green, crustose and frondose groups).

2. Algae can occupy any vacant space in the plot and colonise newly created spaces.

3. Algae are vulnerable to removal during background disturbance processes (Ostrander et al., 2000).

4. Algae cannot out compete and overgrow healthy corals (Bak et al., 1977; de Ruyter van Steveninck et al., 1988; McCook et al., 2001; Meesters et al., 1994; Meesters et al., 1997), nor can they can prevent coral settlement by the pre-emption of space, as corals are assumed to recruit to cryptic environments and vertical surfaces (Rylaarsdam, 1983) while algae grow on horizontal surfaces.

5. Algae can outcompete bleached corals and can overgrow them (Diaz-Pulido and McCook, 2002; McCook et al., 2001; Shulman and Robertson, 1996).

Further 'rules', also based on literature, reflect the physiological effects of bleaching on the life history attributes of corals:

6. A coral colony in a bleached state either returns to a healthy state or dies.

7. If a coral colony is bleached it remains bleached for a year (matching the year cycles of the model). It has been documented that colonies can remain bleached for up to nine months after initial onset (Fitt et al., 1993), though physiological impacts can last for more than a year e.g. impaired reproduction (Sheppard et al., 2002; Szmant and Gassman, 1990).

8. Coral species exhibit differential susceptibility to bleaching (Goreau, 1992; Lang et al., 1992; Lang et al., 1988; Meesters and Bak, 1993; Williams and Bunkley-Williams, 1988).

9. Colonies within a species have equal probabilities of bleaching regardless of colony size.

10. Within a single species population, colonies will not bleach identically (Edmunds, 1994; Lang et al., 1992; Lang et al., 1988; Meesters and Bak, 1993), Ernesto Weil, pers. comm.). Reasons for this are unclear, but are attributable partly to the different genetic makeup of individuals (Edmunds, 1994), their symbiotic zooxanthellae (Kinzie et al., 2001; McField, 1999), and differences in microhabitat surrounding colonies.

11. While a coral colony is in a bleached state, it will not grow (Goreau and Macfarlane, 1990; Leder et al., 1991), reproduce (Omori et al., 2001; Szmant and Gassman, 1990; Witman, 1992), or repair damaged tissue (Mascarelli and Bunkley-Williams, 1999; Meesters and Bak, 1993) and its competitive abilities are impaired (Diaz-Pulido and McCook, 2002; McCook et al., 2001; Shulman and Robertson, 1996).

6.2.2. Integration of algae into the model

Unlike corals, algae were programmed to occupy all bare substratum at the beginning of each year. This avoided the need to attribute a recruitment rate (difficult for such a varied group), and simulates algal behaviour on reefs where every available space is usually colonised by some type of alga. Algal growth rate was initially set at 1 cm yr^{-1}, but this was later adjusted to test for sensitivity of the modelled coral community

to this parameter. The only other life history attribute included for algae was a high probability of mortality, making algae vulnerable to background disturbance. Trials of 3 replicates to 50 years were carried out to confirm that under non-warming circumstances, the presence or absence of algae did not influence the community structure of corals (Figure 6.1). No significant differences were found between coral community compositions of trials with algae and without algae included in the model (one-way ANOSIM: Global R = -0.185, p = 0.800).

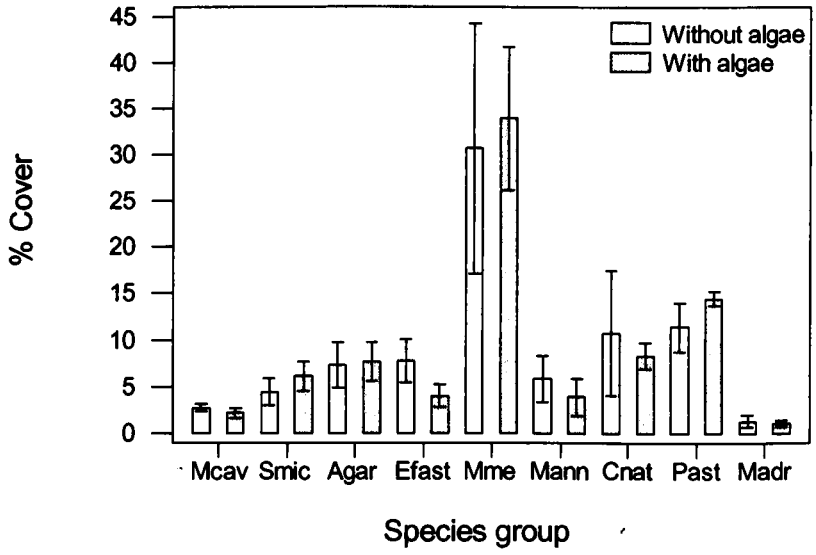


Figure 6.1 Comparison of coral community composition at 50 years with and without algae included in the model (percent cover of corals by group, mean ± 1SD, n = 3 replicates). Mcav denotes *Montastraea cavernosa*, Smic - *Stephanocoenia michelinii*, Agar – *Agaricia* spp., Efast – *Eusmilia fastigiata*, Mme – *Meandrina meandrites*, Mann – *Montastraea annularis*, Cnat – *Colpophyllia natans*, Past – *Porites astreoides*, Madr – *Madracis* spp.

6.2.3. Determination of parameter values for coral bleaching

Reports of bleaching in the Western Atlantic region were reviewed, and coral species ranked according to susceptibility to bleaching, between 0 and 5, dependent on the proportion of colonies within a species population exhibiting bleaching to any

degree[7] (0, no bleaching observed, 1, <10%, 2, 11-25%, 3, 26-50%, 4, 51-75% and 5, 76-100%) (Table 6.1). This was tabulated with other attributes from each report, including the date, location, and approximate number of degree heating months (DHM) which caused the bleaching (extracted from temperature charts on the NOAA website)[8]. From this, each species was assigned an average index value for each level of event (mean DHM) (Table 6.2); this was an estimation of the relative vulnerability to bleaching of each species during four well-reported warming events.

[7] Some reports categorise bleaching as paling (or blanching), mottled or bleached patches, total colony bleached.

[8] http://orbit-net.nesdis.noaa.gov/orad/sub/sst_series_24reefs.html

Table 6.1 Coral bleaching during recent warming events, from multiple sources.

Source	MMM SST[1]	DHM[2]	Location	Cn	Ma	Ag	Pa	Md	Mc	Mm	Sm	Ef
1987												
Lang 1992	28.2	12	St Croix	5	1							
Lang 1992	29.2	8	Bahamas		1							
Lang 1992	29.2	8	Bahamas		1							
Lang 1992			Venezuela	1	2	3						
Lang 1992			Venezuela	1	1	3	1					
Meesters & Bak 1993			Curacao	0	5	0	3	0	2	3	4	
Fitt 1993	29.3	4	Florida		5							
Ghiold & Smith		8	Caymans	5	5	4			2			
Lang et al. 1988	29.2	8	Bahamas		5	5	5	2	3	0	5	0
1988												
Cook et al. 1990		12	Bermuda		3		2		1			
1995												
McField 1999	28.9	4	Belize		5	3	2		3			
McField 1999	28.9	4	Belize	0	5	3		1	2	1		2
1998												
Kramer & Kramer 2000	28.9	8	MABRS[3]	1	3	1	1	2	1	0	2	
Wilkinson 1998[4]		8	Bahamas						0			
Wilkinson 1998[4]			Bonaire			5						
Wilkinson 1998[4]			Brazil			5						
Wilkinson 1998[4]		8	Jamaica		4							
Wilkinson 1998[4]		8	Mexico		5							
Wilkinson 1998[4]		8	Florida	3	4	3	3	3	3	3	3	3
Wilkinson 1998[4]		12	USVI	3	3	3	3					
Wilkinson 1998[4]		12	USVI	4	4	4	4					
Wilkinson 1998[4]		8	Belize		4	5	5					
Wilkinson 1998[4]		8	Cayman Islands		4				1			

[1] MMM (Maximum Monthly Mean) (from NOAA website: http://orbit-net.nesdis.noaa.gov/orad/sub/sst_series_24reefs.html).

[2] DHM (Degree Heating Months) Estimated from Degree Heating Week charts on NOAA website

[3] MABRS - Meso-American Barrier Reef System (Yucatan Mexico, Belize, Guatemala and N. Honduras)

Cn – *Colpophyllia natans*, Ma – *Montastraea annularis* complex, Ag – *Agaricia* spp., Pa – *Porites astreoides*, Md – *Madracis* spp. Mc – *Montastraea cavernosa*, Mm – *Meandrina meandrites*, Sm – *Stephanocoenia michelinii*, Ef – *Eusmilia fastigiata.*

[4] http://www.aims.gov.au/scr1998.

Table 6.2 Mean bleaching indices for coral species during each documented warming event, with number of reports (n). DHW = degree heating weeks.

	1987		1988		1995		1998	
	Mean	n	Mean	n	Mean	n	Mean	n
DHW	8.0	6	12	1	4	2	8.89	9
C. natans	2.4	5		0	0.0	1	2.8	4
M. annularis	2.9	9	3	1	5.0	2	3.9	8
Agaricia spp.	3.0	5		0	3.0	2	3.7	7
P. astreoides	3.0	3	2	1	2.0	1	3.2	5
Madracis spp.	1.0	2		0	1.0	1	2.5	2
M. cavernosa	2.3	3	1	1	2.5	2	1.3	4
M. meandrites	1.5	2		0	1.0	1	1.5	2
S. michelinii	4.5	2		0		0	2.5	2
E. fastigiata	0.0	1		0	2.0	1	3.0	1

Corals were divided into four groups of decreasing vulnerability to bleaching and thermally induced mortality (Table 6.3). The probability of a colony either bleaching or dying was then estimated for each of the four susceptibility groups at three levels of warming event intensity (Figure 6.2).

Table 6.3 Susceptability ranking of corals to bleaching and mortality.

Coral susceptibility group	Species
Susceptible (1)	*Stephanocoenia michelinii, Montastraea annularis*
Moderately susceptible (2)	*Agaricia* spp., *Porites astreoides*
Moderately resistant (3)	*Montastraea cavernosa, Colpophyllia natans, Madracis* spp.
Resistant (4)	*Eusmilia fastigiata, Meandrina meandrites*

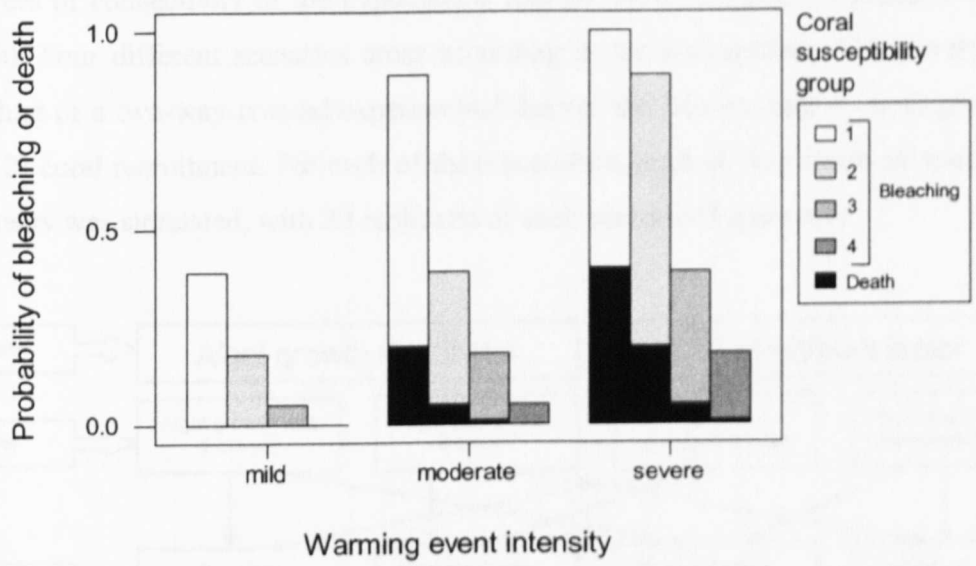


Figure 6.2 Probabilities of coral colonies bleaching or dying during warming events for the four coral susceptibility groups; 1 = susceptible, 2 = moderately susceptible, 3 = moderately resistant and 4 = resistant, for three levels of warming event. Black bars indicate the proportion of the population undergoing total colony mortality, while white and grey bars indicate bleaching and subsequent recovery.

6.2.4. Experimental design

All simulations began with a vacant plot as before, and run for 300 years to stabilise before a warming event was applied. These data were not used in the analyses and zero on all graphs corresponds to the year immediately prior to the disturbance event, and 100 years corresponds to the end of the simulation. Four levels of warming event were then applied; 1) no warming event, 2) mild warming event (simulating 1987), 3) moderate warming event (simulating 1998) and 4) severe warming event (based on laboratory experiments, Fitt and Warner, 1995). Model output was taken as percent cover from immediately prior to the simulated warming event (year 0) until the end of the simulation (100 years).

6.2.4.1. Varying coral recruitment rate and algal growth rate

Scenarios were designed to investigate the influence of environmental factors acting locally that might operate synergistically with warming events to intensify the impact

of such events on the coral community. Specifically these scenarios were enhanced growth rate of algae (an indication of system sensitivity to algal growth rate and potential reef nutrification) and changes in coral recruitment (simulating differing degrees of connectivity of the hypothetical reef on which the plot is located to other reefs). Four different scenarios arose according to the assumptions. These were the product of a two-way crossed experimental design: the factors were 1) algal growth, and 2) coral recruitment. For each of these scenarios, each of four levels of warming intensity was simulated, with 20 replicates of each scenario (Figure 6.3).

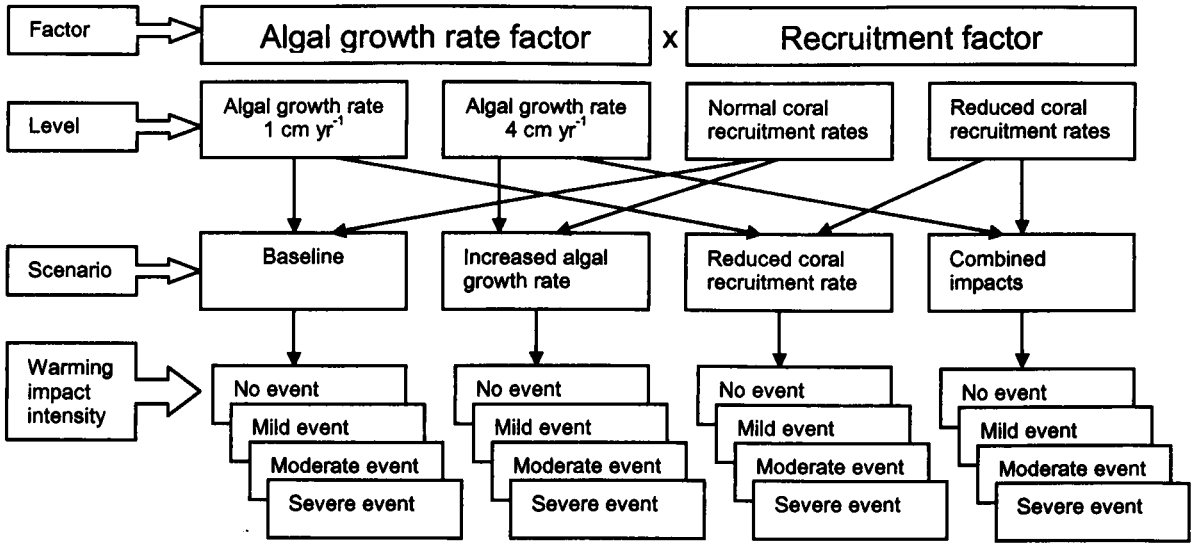


Figure 6.3 Experimental design. Two factor crossed design to generate four scenarios, each of which were tested at four levels of warming event intensity.

Algal growth was examined at 1 cm yr^{-1} and 4 cm yr^{-1}. As a starting point, the lower value was assigned, and in order to determine if coral community structure was influenced by changes in this parameter, a second rate of 4 cm yr^{-1} was subsequently tested.

Coral recruitment was also investigated at two levels: normal (i.e. not impacted by warming events) and reduced. The capacity of a reef to recover from impacts depends to a large extent on its 'supply-side' ecology (fecundity, larval dispersal, settlement, recruitment, *sensu* Lewin, 1986) and this in turn is influenced by the connectivity (physical linkage through the movement of water masses) of the reef. If a reef has low connectivity (i.e. mostly self-seeding) and corals are bleached during a warming event, it follows that the pool of recruits will be reduced. In order to

simulate reduced coral recruitment, the recruitment rate of a coral species was decreased by a factor relative to the proportion of the population bleached (e.g. during a moderate warming event, 18% of *Colpophyllia natans* colonies are bleached. Under normal conditions, the recruitment rate of this species is 1.7 spat 9 m^2 yr^{-1}, thus during the warming event recruitment rate will decrease by 18% to 1.39 spat 9 m^2 yr^{-1}). This reduction in coral recruitment was only applied during the year of the warming event and the subsequent year recruitment was returned to pre-warming levels (see Assumption 6).

6.2.4.2. Community analyses over time

Percent cover data were used to assess the impacts of warming events on coral community structure, as in this particular instance, this type of data was found to be sensitive to changes from disturbances than either colony counts or mean colony sizes by species. Bray-Curtis similarity matrices were constructed using all 20 replicates from each scenario at each level of warming event. Data were not transformed. Differences between years were analysed as the community recovered using one-way analyses of similarity (ANOSIM). The recovery point was defined as that where the community was no longer statistically significantly different from its state before impact using pair-wise comparisons from one-way ANOSIM results. Recovery was shown as trajectories on multidimensional scaling (MDS) ordinations generated from the matrices. Minimum stress values are given for MDS ordinations, indicating the strength of the two-dimensional representation of multidimensional similarities; low stress values signify good representations. Comparisons between scenarios were made using two-way crossed ANOSIMs (time x scenario).

6.3. Results

The baseline scenario (algal growth rate of 1 cm yr^{-1} and normal rates of coral recruitment) was explored for each of the four warming event intensities. Then the influences of varied algal growth rates and coral recruitment rates were examined.

6.3.1. Baseline scenario (algal growth rate of 1 cm $year^{-1}$ and normal coral recruitment)

6.3.1.1. No warming event

When the model was run without a warming event, the community stabilised at approximately 150 years after initiation, and though this equilibrium state had variably, it persisted for the remainder of the simulation (Figure 6.4). The modelled coral community was dominated by *Montastraea annularis*, *M. cavernosa*, *Agaricia* spp. and algae, with all other species represented but at covers of less than 10%.

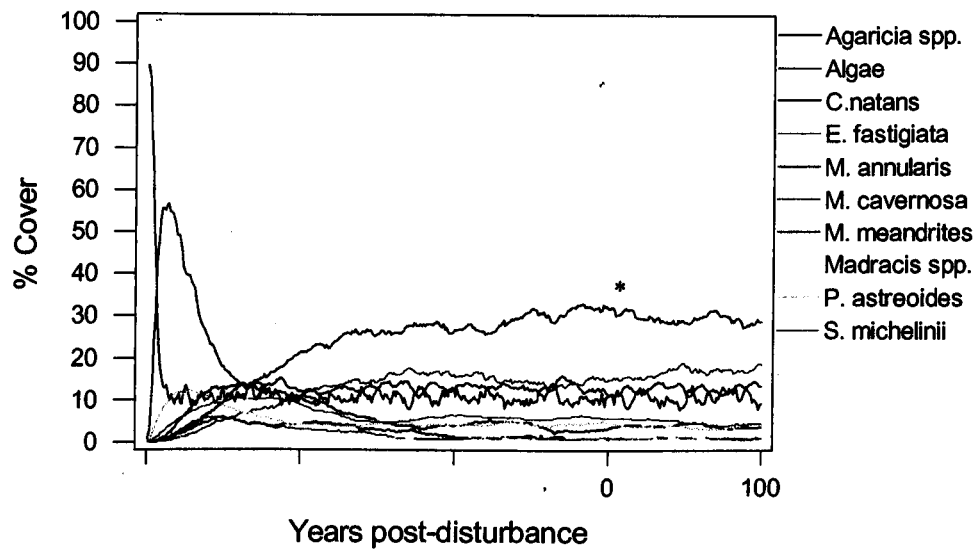


Figure 6.4 Baseline scenario – no warming event. Community composition of the modelled plot (mean of 20 replicates). Simulation was run for 300 years prior to applying impact (in this case none *) during year 1, and run for a further 100 years.

This highly consistent community structure was confirmed by a one-way ANOSIM over time (carried out on data between 0 and 10 years), (Global R = -0.05, p > 0.999) and pair-wise tests indicate that no community differed significantly from any other (all p values > 0.97).

6.3.1.2. Mild warming event

The impact of a mild warming event was not detectible on the community structure (Figure 6.5). Mortality induced by the warming event was not sufficient to distinguish the event from background mortality processes.

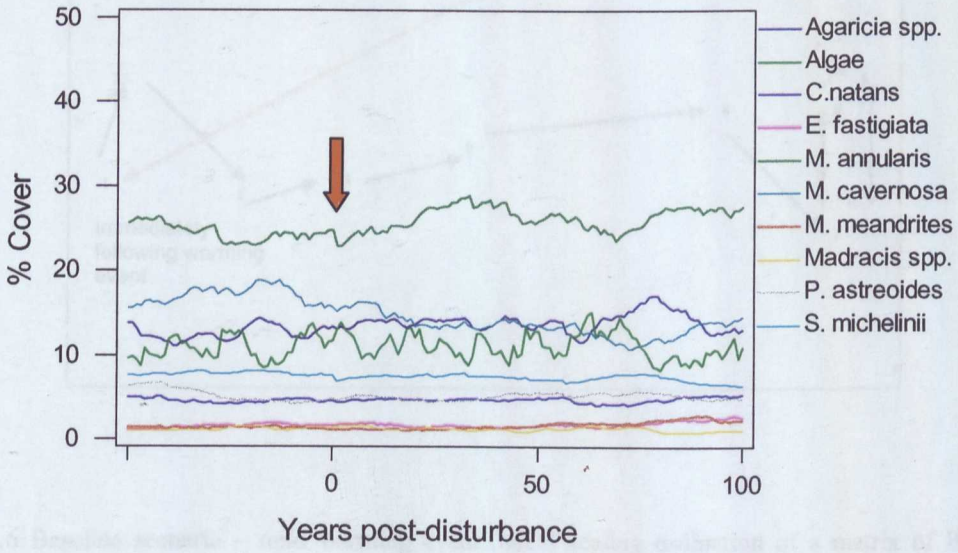


Figure 6.5 Baseline scenario – mild warming event. Community composition of the modelled plot with a mild warming event applied during year 1 (red arrow), mean of 20 replicates.

The lack of any significant effect is confirmed by a one-way ANOSIM over time (Global R = -0.097, p > 0.999), and further confirmed by pair-wise comparisons (Table 6.4).

Table 6.4 Baseline scenario – mild warming event. Statistical significance of pair-wise comparisons of pre-warming community structure (year 0) with communities from subsequent years, derived from one-way ANOSIM (using all replicates).

Year	1	2	3	4	5	6	7	8	9	10
R	-0.048	-0.042	-0.055	-0.054	-0.046	-0.035	-0.029	-0.04	-0.046	-0.046
p	0.964	0.935	0.986	0.985	0.962	0.863	0.827	0.936	0.968	0.979

The MDS ordination graphically showed the greatest community transition occurred during the warming event, suggesting that there was some impact on the coral community, but not sufficient to be distinguished from background mortality processes (Figure 6.6). (The MDS ordination is dimensionless, i.e. the trajectory fills the plot area. It is shown later that this community change is very small compared with changes following greater impacts).

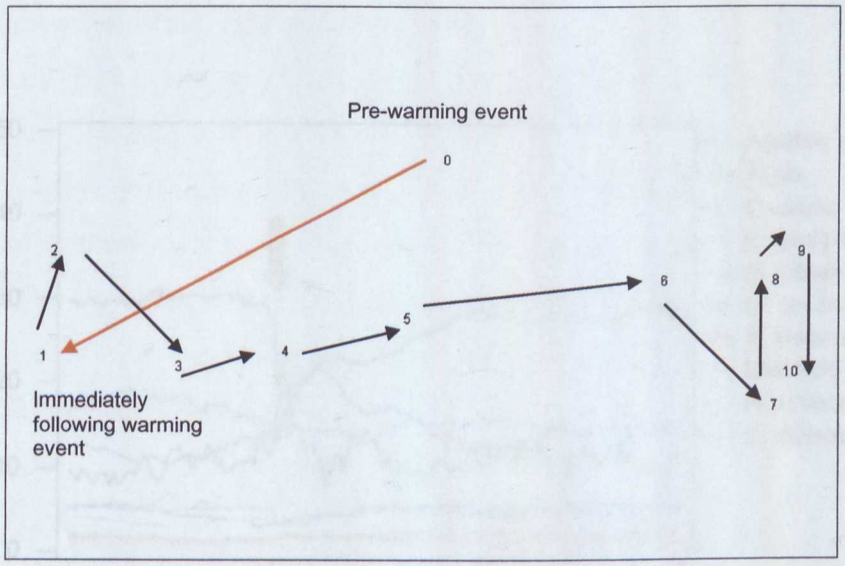


Figure 6.6 Baseline scenario – mild warming event. MDS scaling ordination of a matrix of Bray-Curtis similarity indices of species cover data indicating structural similarities of modelled coral community with a mild warming event applied during year 1 (mean of 20 replicates) Numbers indicate years post-warming, red arrow denotes community trajectory during the warming event, black arrows denote community trajectories at 1 year intervals following the warming event. Minimum stress for the best two-dimensional configuration is 0.02.

6.3.1.3. Moderate warming event

The moderate warming event produced a greater impact. Community composition changed dramatically and immediately; algal abundance increased from 12.6±6.3% to 17.9±6.8% (>40% increase) and there was a reciprocal decrease in certain coral groups, notably *Montastraea annularis* and *Stephanocoenia michelinii* (33% and 39% relative decrease from their original abundances respectively). Other species decreased but by lower amounts; *Porites astreoides* by 13% and *M. cavernosa* and

Agaricia spp. both by <10%. Other species were not affected. Following the warming event, community structure recovered rapidly. *Agaricia* spp. increased in abundance, and by 12 years after the warming event, it occupied 22.2±6% of the plot (almost twice its pre-warming abundance). At this time, cover of algae had declined to levels comparable to their pre-warming condition. By then all other species with the exception of *M. annularis* and *S. michelinii,* had recovered to their former levels. These two coral groups did not fully recover until around 43 and 29 years after disturbance for *S. michelinii* and *M. annularis* respectively.

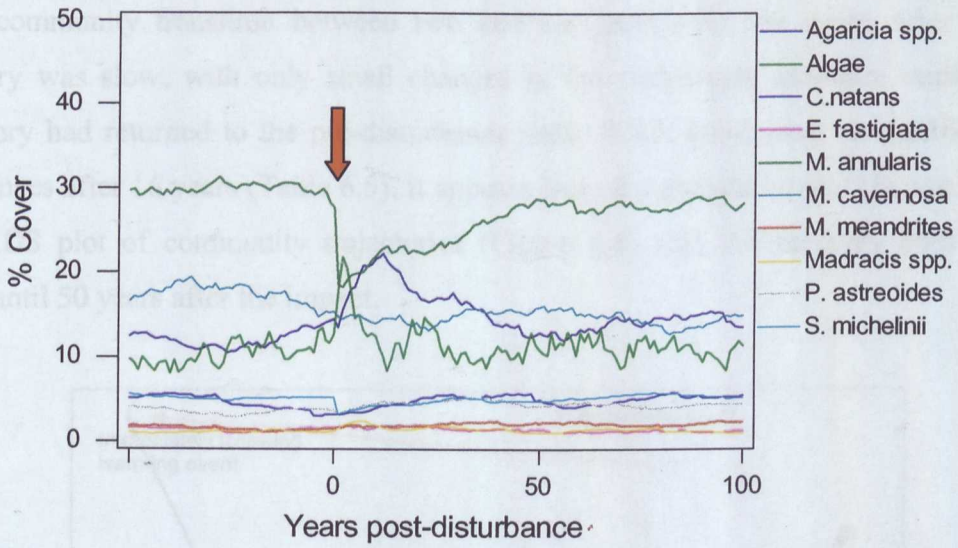


Figure 6.7 Baseline scenario – moderate warming event. Community composition of the modelled plot with a moderate warming event applied during year 1 (red arrow) mean of 20 replicates.

Community composition was significantly different over time (one-way ANOSIM: R = 0.042, $p < 0.001$), and pair-wise comparisons confirm that the community remained significantly different from the pre-warming state (0 years) until 16 years after the event (Table 6.5). Shortly after the disturbance event (4-6 years), the pair-wise comparisons did not show significant differences from the pre-disturbance state, due to the large variability generated by the disturbance.

Table 6.5 Baseline scenario – moderate warming event. Statistical significance of pair-wise comparisons of the pre-warming community structure (year 0) with communities from subsequent years, derived from one-way ANOSIM (using all replicates).

Year	2	4	6	8	10	12	14
R	0.158	0.047	0.049	0.07	0.077	0.081	0.069
P	0.002*	0.071	0.067	0.026*	0.041*	0.025*	0.04*

Year	16	18	20	30	40	50
R	0.038	0.027	0.028	0.025	-0.036	-0.022
P	0.133	0.163	0.172	0.216	0.895	0.74

* indicates significant difference

The community shows a marked change in structure immediately following the warming event (between years 0 and 2) (Figure 6.8). Then there was a period of rapid community transition between two and six years after the event, after this recovery was slow, with only small changes in the community structure until the trajectory had returned to the pre-disturbance state. While there were no significant differences after 16 years (Table 6.5), it appears from the abundance plot (Figure 6.7) and MDS plot of community trajectories (Figure 6.8) that full recovery does not occur until 50 years after the impact.

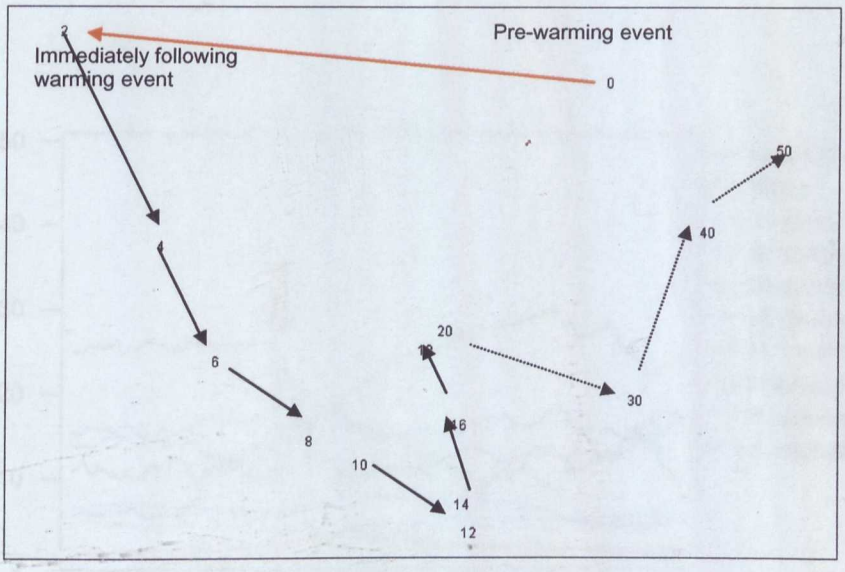


Figure 6.8 Baseline scenario – moderate warming event. MDS ordination of a matrix of Bray-Curtis similarity indices of species cover data indicating structural similarities with a moderate warming event applied during year 1 (mean of 20 replicates). Numbers indicate years, red arrow denotes community trajectory during the warming event, solid arrows denote community trajectories at 2 year intervals following the warming event, broken arrows denote 10 year intervals. Minimum stress for the best two-dimensional configuration is 0.02.

6.3.1.4. Severe warming event

A severe warming event had similar effects to a moderate event. Immediately following the event, the greatest declines in abundance were seen in *Montastraea annularis* and *Stephanocoenia michelinii,* 43% and 53% of their pre-warming levels respectively. Other large declines were seen in *Porites astreoides*, *M. cavernosa* and *Agaricia* spp. (36%, 14% and 28% decreases respectively). Other species also declined, but by less than 7%, with the exception of *Madracis* spp. and algae which both increased in abundance (31% and 100% respectively), (Figure 6.9). As with the moderate warming event, community recovery was characterised by an increase in Agariciid abundance (from 9.83 ± 4.1% to 19.4 ± 4.5% after eight years, approximately a 2-fold increase, greater than the initial cover of 13.72 ± 5.6%). By ten years, the abundance of *Agaricia* spp. was already declining, as was algal abundance, but other groups were showing signs of recovery and some such as *P. astreoides* had recovered to their pre-warming levels of abundance.

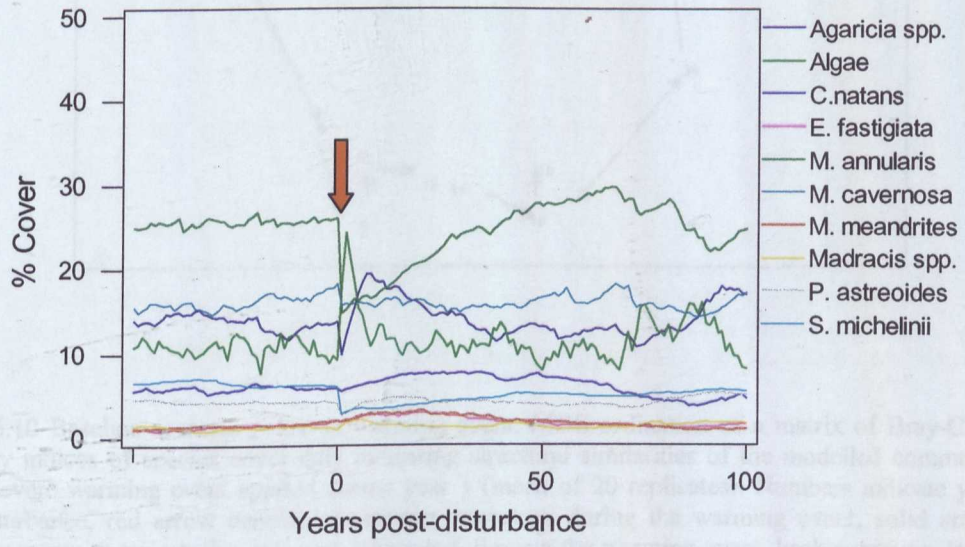


Figure 6.9 Baseline scenario – severe warming event. Community composition of the modelled plot with a severe warming event applied during year 1 (red arrow), mean of 20 replicates.

These changes in community structure over time were highly significant (one-way ANOSIM: Global R = 0.071, p = 0.001). Pair-wise comparisons show that the community was significantly different from the pre-warming state for 16 years (Table 6.6).

Table 6.6 Baseline scenario – severe warming event. Statistical significance of pair-wise comparisons of pre-warming community structure (year 0) with communities from subsequent years, derived from one-way ANOSIM (using all replicates).

Year	2	4	6	8	10	12	14
R	0.44	0.263	0.199	0.171	0.126	0.085	0.077
P	0.001*	0.001*	0.001*	0.001*	0.007*	0.018*	0.033*

Year	16	18	20	30	40	50
R	0.032	0.048	0.021	-0.026	-0.022	-0.066
P	0.186	0.093	0.2	0.781	0.736	0.999

* indicates significant difference

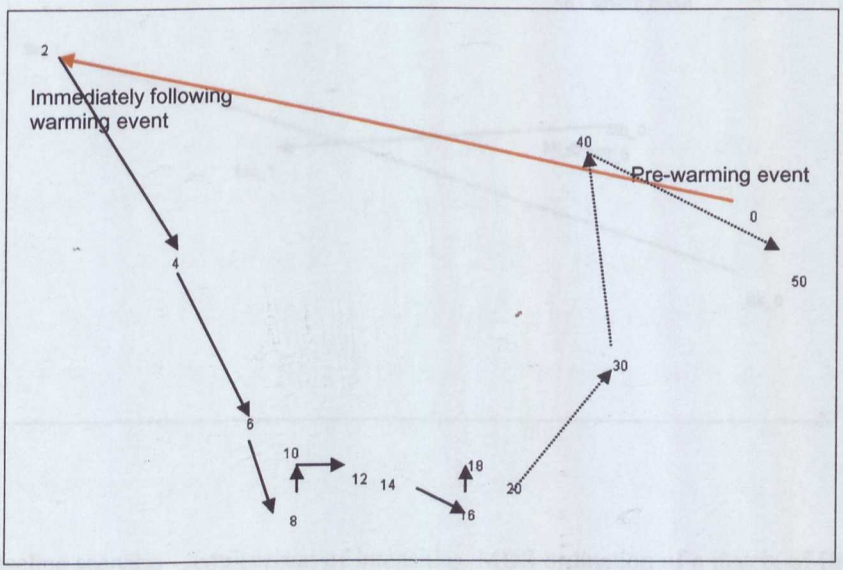


Figure 6.10 Baseline scenario – severe warming event. MDS ordination of a matrix of Bray-Curtis similarity indices of species cover data indicating structural similarities of the modelled community with a severe warming event applied during year 1 (mean of 20 replicates). Numbers indicate years post-disturbance, red arrow denotes community trajectory during the warming event, solid arrows denote community trajectories at 2 year intervals following the warming event, broken arrows denote 10 year intervals. Minimum stress for the best two-dimensional configuration is 0.03.

Recovery occurred in two stages, similar to that following a moderate warming event. An initial period of rapid recovery (between two and six years post-

disturbance) was followed by a slower restoration to the starting position after about 40 years (Figure 6.10).

6.3.1.5. Comparison between intensities of warming events

Disturbance intensity had an influence on community response, the larger the event, the further the displacement of the community, though this response was not linearly proportional to warming intensity. To compare the three effects with one another, a MDS plot (Figure 6.11) shows the immediate responses to the impacts at the same scale. All coral community transitions occurred in the same direction, however, during a severe event approximately twice as many coral colonies undergo total colony mortality (from all coral susceptibility groups) compared to a moderate event.

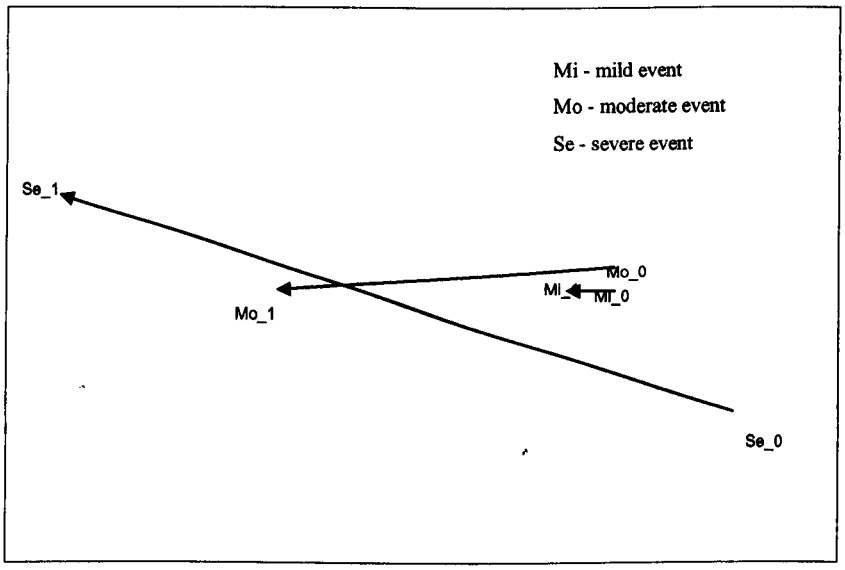


Figure 6.11 Baseline scenario – comparison of intensities. MDS ordination of a matrix of Bray-Curtis similarity indices of species cover data indicating community transitions pre and immediately post-warming event (0 and 1 years respectively). Arrows connect sequential communities for three levels of warming event (mean of 20 replicates). Minimum stress for the best two-dimensional configuration is 0.01.

Total coral cover from moderate and severe events was compared over time (one-way ANOVAs: $F = 4.37_{(df = 10)}$, $p < 0.001$, $F = 9.15_{(df = 10)}$, $p = < 0.001$ for moderate and severe events respectively. Recovery to the pre-disturbance state was complete two years after a moderate warming event and four years after a severe warming event, (determined by Tukey pair-wise comparisons).

6.3.2. Effect of increased algal growth

The simulations were repeated for an increased algal growth rate of 4 cm yr^{-1}, and for each level of impact compared to the baseline scenario. There were no detectible differences in controls (simulations with no warming event), confirming that under non-impact conditions changed algal growth rate by itself had no effect (Table 6.7).

Algal growth rate appeared to influence coral community structure following a moderate warming event, but these differences were not significant (Table 6.7). There was no peak in the abundance of *Agaricia* spp. though decreases in *M. annularis* abundance were comparable (9.27 ± 7.16% and 9.40 ± 6.92% between 0 and 1 years, for algal growth rates of 1 cm yr^{-1} and 4 cm yr^{-1} respectively (mean difference ± 95% confidence interval) (Figure 6.12). The initial increase in algal abundance was greater with increased algal growth rate; 5.29 ± 4.22% compared to 10.67 ± 3.09% for algal growth rate 1 cm yr^{-1} and 4 cm yr^{-1} respectively (mean difference ± 95% confidence interval).

The effect of algal growth rate on community recovery was more pronounced following a severe warming event (Figure 6.12b). Immediately following the event there was a large increase in algae: 9.13 ± 2.95% compared to 22.78 ± 5.07% between 0 and ten years for simulations with algal growth rates of 1 and 4 cm yr^{-1} respectively, (mean difference ± 95% confidence interval). After a lag of six years, there was a peak in *Agaricia* spp. This was much larger than the peak in *Agaricia* spp. during the baseline scenario simulation (Figure 6.9), and lasted longer.

Table 6.7 Increased algal growth. Multivariate comparisons of community structure for increased algal growth rate scenario and baseline scenario for the four levels of warming event; two-way crossed ANOSIM (time x algal growth rate).

Warming Event Level	Factor			
	Time		Algal growth rate	
	R	p	R	p
None	-0.07	> 0.999	0.031	0.146
Mild	-0.044	> 0.999	0.007	0.249
Moderate	0.011	0.05*	0.005	0.685
Severe	0.173	< 0.001*	0.135	< 0.001*

* indicates significant difference

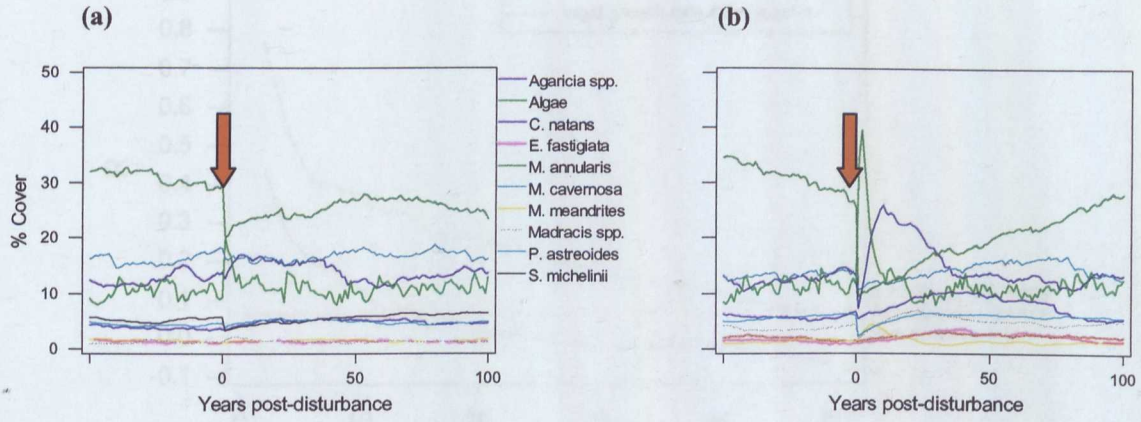


Figure 6.12 Increased algal growth. Community response to warming events (a) moderate event, and (b) severe event, applied during year 1 (red arrows), mean of 20 replicates.

Algal growth rate influenced recovery time (one-way ANOSIM: $R = 0.274$, $p < 0.001$). The earliest community showing complete recovery under conditions of increased algal growth occurred after 50 years, compared with 16 years (baseline scenario, algal growth rate 1 cm yr^{-1}) (Figure 6.13, above the threshold line shows communities significantly different from the initial state; the point where the threshold is crossed marks statistically complete recovery). The shapes of the pair-wise comparison curves are extremely similar, showing rapid recovery (steep initial part) between two and six years, and then the gradient becomes shallower, indicating slower recovery for the remainder of the simulation. However, the pre and post-warming communities are markedly more dissimilar for the simulation with high algal growth, and continued to be more dissimilar throughout the simulation, though the shape of recovery is comparable to the baseline scenario.

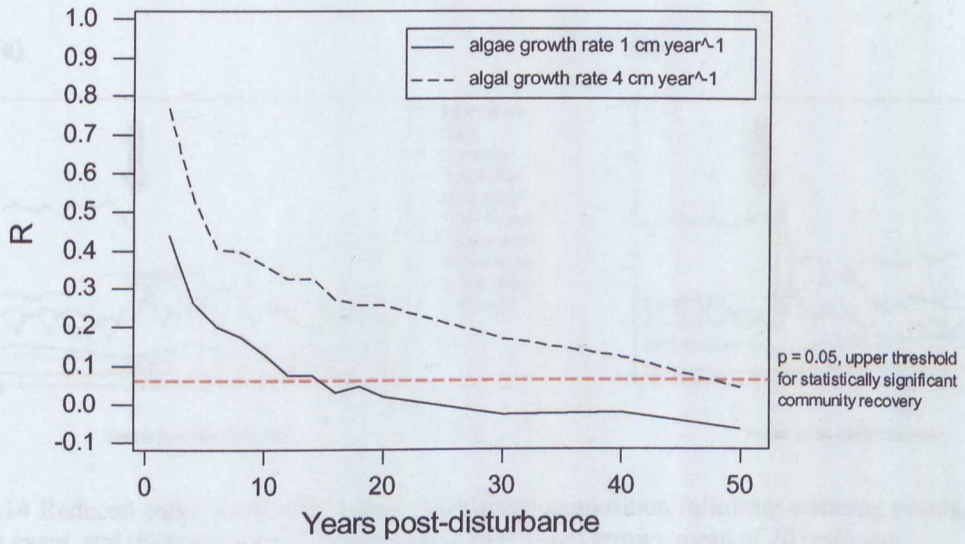


Figure 6.13 Increased algal growth – severe warming event. Statistical significance of pair-wise comparisons (R) of pre-warming community structure (year 0) with communities from subsequent years, derived from one-way ANOSIM (using all replicates). Community comparisons above the p = 0.05 threshold are significantly different to the pre-disturbance state, the point where the threshold is crossed denotes complete recovery.

6.3.3. Effect of reduced coral recruitment

The effect of reduced coral recruitment following warming events was then examined. Following a mild warming event, reduced recruitment rate had no influence on the community structure (Table 6.8). It did appear to influence recovery following a moderate warming event (Figure 6.14a). However, these differences were not significant at a community level (Table 6.8). Reduced recruitment prevented *M. annularis* from regaining its former abundance. Also *Agaricia* spp. did not decline to pre-warming abundance levels after peaking at six years, but remained higher for the remainder of the simulation. Pair-wise comparisons showed that communities remain significantly different following the warming event until 18 years later, compared with 16 years under normal coral recruitment rates.

Table 6.8 Reduced coral recruitment. Multivariate comparisons of community composition between reduced recruitment scenario and baseline scenario at three levels of warming event; two-way crossed ANOSIM (time x recruitment type).

Warming Event Level	Factor			
	Time		Coral recruitment	
	R	P	R	p
Mild	-0.047	> 0.999	0.011	0.138
Moderate	0.02	0.006*	0.005	0.241
Severe	0.097	> 0.001*	0.037	> 0.001*

* indicates significant difference

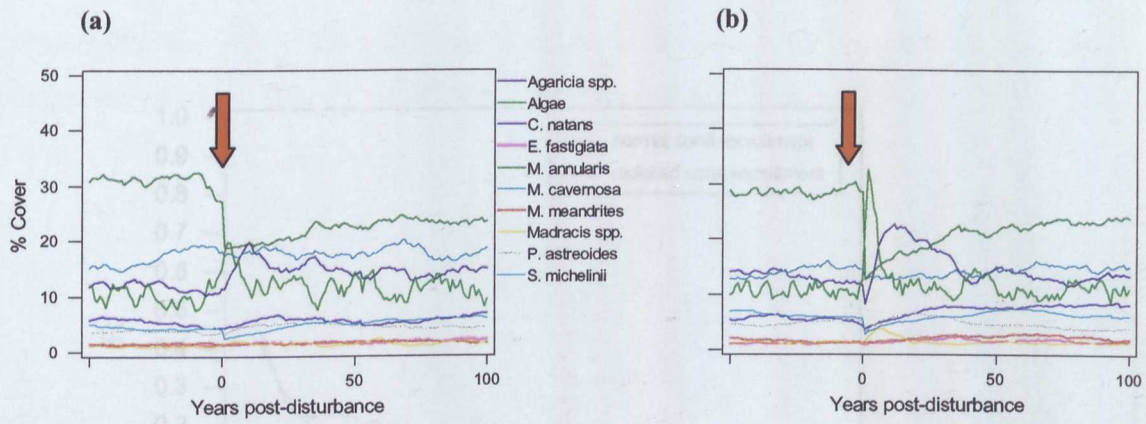


Figure 6.14 Reduced coral recruitment. Coral community composition following warming events, (a) moderate event, and (b) severe event, applied during year 1 (red arrow), mean of 20 replicates.

Reduced coral recruitment strongly influenced recovery following a severe warming event (Table 6.8) (one-way ANOSIM: R = 0.124, p = 0.01). Primarily there was a much greater algal abundance. Also there were some differences in the abundances of *Agaricia* spp.; the peak was larger and extended for a longer time period, and the maximum abundance occurred at 12 years after the warming event, compared with 8 years in the baseline scenario. Finally, the recovery of *M. annularis* abundance appeared to be slower (Figure 6.14b).

Pair-wise comparisons derived from the ANOSIM reveal the community was significantly different to the post-warming community until at least 40 years after the event (all community comparisons above the p = 0.05 threshold are significantly different, and where the line crosses below the threshold indicates complete recovery, Figure 6.15). This is a substantially longer recovery time than required under normal coral recruitment (baseline scenario, 16 years). Also the recovery curves are different in shape, after the initial 3 years, the slope of the curve for reduced recruitment is shallower than that for normal recruitment. Thus loss of recruits greatly slows recovery.

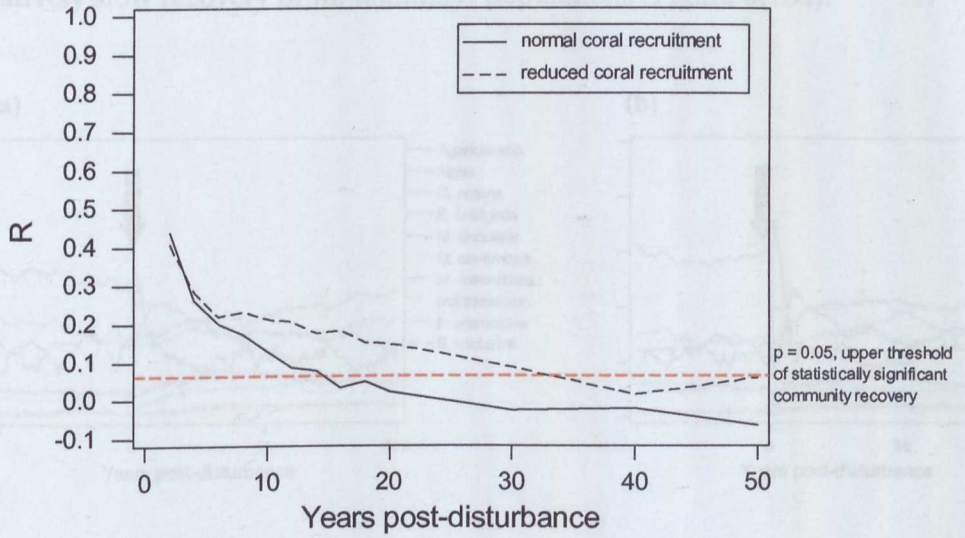


Figure 6.15 Impacted recruitment rate – severe warming event. Statistical significance of pair-wise comparisons (R) of pre-warming community structure (year 0) with communities from subsequent years, derived from one-way ANOSIM (using all replicates). Community comparisons above the p = 0.05 threshold are significantly different to the pre-disturbance state, the point where the line is crossed denotes complete recovery.

6.3.4. Combined effect of both increased algal growth and reduced coral recruitment

Simulations where no warming event was applied or with a mild event, showed no difference in community structure under the combined scenario (both increased algal growth and reduced coral recruitment) (Table 6.9).

Table 6.9 Increased algal growth and reduced coral recruitment. Multivariate comparisons of community composition for scenario with both increased algal growth rate and impacted recruitment and the baseline scenario; two-way crossed ANOSIM (time x scenario).

Warming Event Level	Factor			
	Time		Scenario	
	R	P	R	p
None	-0.05	> 0.999	0.004	0.315
Mild	-0.044	> 0.999	-0.001	0.513
Moderate	0.045	< 0.001*	0.045	< 0.001*
Severe	0.126	< 0.001*	0.021	< 0.001*

* indicates significant difference

Moderate warming did influence the recovering community. Community composition showed a large increase in algal abundance. Another feature was the comparatively slow recovery of *M. annularis* populations (Figure 6.16a).

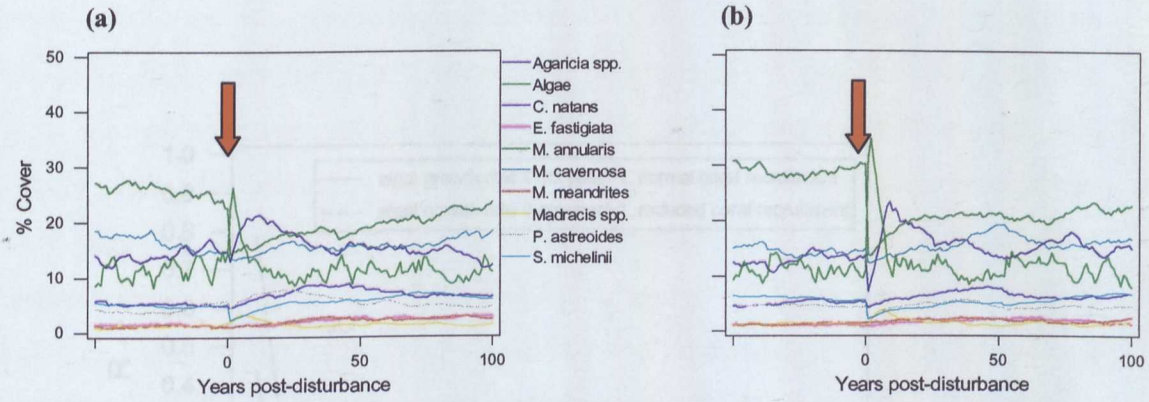


Figure 6.16 Combined effect of increased algal growth and reduced coral recruitment. Coral community composition following warming events, (a) moderate event, and (b) severe event, applied during year 1 (red arrow), mean of 20 replicates.

Although these differences in community structure were significant over time (one-way ANOSIM: $R = 0.048$, $p < 0.001$, subsequent pair-wise comparisons show that the community was indistinguishable from the pre-warming state very rapidly (Table 6.10). This is likely to be a consequence of very high variance within the dataset.

Table 6.10 Combined effect of increased algal growth and reduced coral recruitment – moderate warming event. Statistical significance of pair-wise comparisons of pre-warming community structure (year 0) with communities from subsequent years, derived from one-way ANOSIM (using all replicates).

Year	2	4	6	8	10	12	14
R	0.115	0.046	0.037	0.06	0.055	0.053	0.042
P	0.013*	0.129	0.154	0.065	0.059	0.088	0.121

Year	16	18	20	30	40	50
R	0.028	0.035	0.005	0.017	0.011	0.003
P	0.183	0.153	0.34	0.257	0.291	0.383

* indicates significant difference

Following a severe warming event, the combined effect of increased algal growth and reduced coral recruitment strongly influenced recovery (Figure 6.16b). Immediately following the event there was a large increase in algal abundance, and the following peak in *Agaricia* spp. was also larger than seen during the baseline scenario (Figure 6.9). The abundance of *Montastraea annularis* never recovered to

its pre-warming abundance. These differences were significant between scenarios and over time (Table 6.9). Full recovery did not occur during the simulation: the community was maintained in an altered state for at least 90 years after the warming event (Figure 6.16b, Figure 6.17).

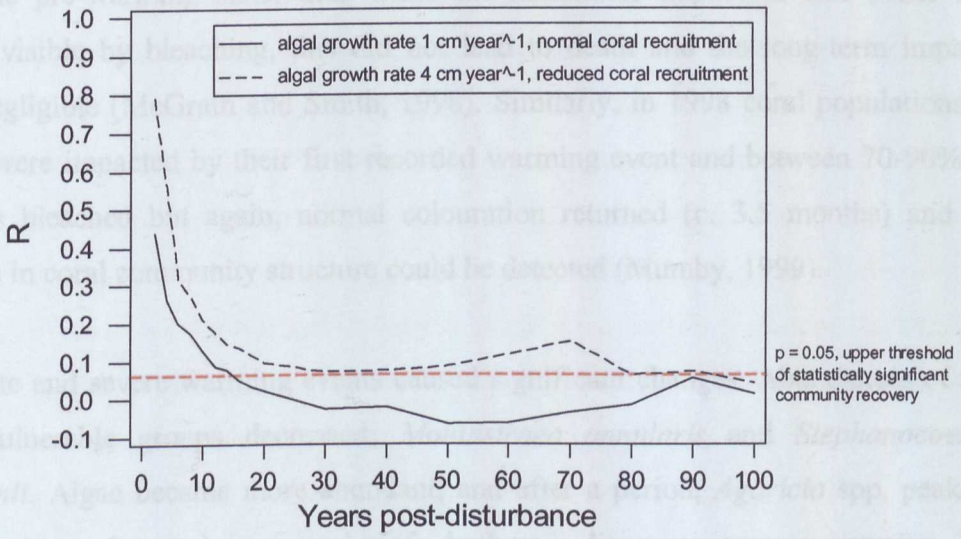


Figure 6.17 Combined effect of increased algal growth and reduced coral recruitment – severe warming event. Statistical significance of pair-wise comparisons of pre-warming community structure (year 0) with communities from subsequent years, derived from one-way ANOSIM (using all replicates) for simulation impacted by a severe warming event.

6.4. Discussion

The modelled coral community demonstrated interesting and complex behaviour following disturbance by a warming event. Initial community responses had strong similarities to real communities following recent warming events, though long-term responses have not yet been quantified for real reefs. This is encouraging, though where the greatest promise lies is in its prediction over longer time frames. Community responses can be divided into two general categories: 1) no impact after mild events and 2) severe disruption after moderate and severe warming events demonstrating the non-linearity of coral community responses to disturbance.

Recovery from single events may take, according to this model, 0 – 90 years depending on the intensity of the event and the local setting of the reef.

The lack of model response to a mild event reflects past real warming events. One month after a warming event in the Bahamas in 1995, 14% of all coral colonies were bleached. Eight months later, however, the community composition was unaltered from the pre-warming state; thus while the immediate impact of this event was clearly visible by bleaching, this did not lead to death and the long-term impacts were negligible (McGrath and Smith, 1998). Similarly, in 1998 coral populations in Belize were impacted by their first recorded warming event and between 70-90% of colonies bleached but again, normal colouration returned (c. 3.5 months) and no changes in coral community structure could be detected (Mumby, 1999).

Moderate and severe warming events caused significant changes. Abundances of the most vulnerable groups decreased; *Montastraea annularis* and *Stephanocoenia michelinii*. Algae became more abundant, and after a period, *Agaricia* spp. peaked. This has been observed on several reefs, both as a direct response to warming, but also in response to other types of disturbances. One year after a warming event in 1994 in the Bahamas, coral cover had declined by 46% and algal cover had increased rapidly by around 160%. In the three years that followed, coral cover remained almost static, but algal cover increased further to more than twice its pre-warming cover, (except during a hurricane that reduced algal cover temporarily) (Ostrander et al., 2000). A similar trend was observed in Panama in the wake of the 1983 warming event (Shulman and Robertson, 1996). Coral cover declined by nearly 50% in the two years following warming. Algae increased during this time period by up to 2-fold and four years later algae started to decline. These results may be confounded by the death of a major herbivore, *Diadema antillarum* during the early 1980s, which allowed macroalgae to persist at high densities for longer periods, but the decline in several other types of algae suggests a pattern similar to that predicted by the model.

There are no reports of increased Agariciid abundance specifically following warming events, but there are cases of this happening after other types of acute disturbance. In Belize, *Acroporas* dominated the central shelf lagoon until white-band disease virtually eliminated them during the mid-1980s. In less than ten years,

reefs were rapidly recolonised by *Agaricia* spp. (and *Porites* spp. to a lesser extent). Reasons given for this were its relatively short-lived, opportunistic life history (Aronson and Precht, 2001). Furthermore, *Agaricia* spp. and *Porites astreoides* have been found to be comparatively resilient to disturbances (hurricanes) by transition matrix modelling (Andres and Rodenhouse, 1993).

Recovery of coral communities following disturbances depends on a number of factors including successional sequence and diversity of the coral reef (Dustan and Halas, 1987); past and present dynamics of the community (Hughes, 1989); environmental tolerances and life history strategies of the dominant species (Fisk and Done, 1985); secondary disturbances such as predation and erosion (Glynn, 1988) and the magnitude of the disturbance (Lasker et al., 1984). In this study, however, the intensity of the event did not seem to greatly affect the recovery time of the baseline scenario (low algal growth and normal coral recruitment) following moderate and severe warming events, although there were differences in the immediate community response to the levels of disturbance. In contrast, results from the scenarios with increased algal growth and reduced coral recruitment showed clear differences in community responses and recovery times following events of increasing intensities.

Moderate and severe impacts caused similar effects. Recovery was rapid initially, but slowed down after 6 years, with the community slowly changing in the direction of the pre-disturbance state. It is difficult to test this against real reef responses in the Caribbean because most monitoring projects only operate for a few years following a disturbance event and the few long term studies that have been carried out on Caribbean reefs have not yet reported a single incidence of recovery (see review by Connell, 1997). Many papers document physiological recovery such as restoration of normal colouration (Fitt et al., 1993; Ghiold and Smith, 1990; Lang et al., 1992; Quinn and Kojis, 1999), but this is not the same as coral community recovery.

One plausible reason why Caribbean reefs have not exhibited recovery following impacts is related to the type and frequency of disturbance; many areas have been subjected to multiple disturbances occurring either simultaneously or sequentially. A famous example is the north coast of Jamaica (Hughes and Connell, 1999; Liddell, 1992). Two major hurricanes struck these reefs in 1980 and 1989, and recovery has

not occurred to date. The lack of recovery has been partly attributed to low herbivore abundances due to over-fishing, contributing to a prolonged bloom of macroalgae. Another factor in the shift in dominance from corals to algae was the die-off of the grazer *Diadema antillarum* in 1983, thus further decreasing herbivore populations. Additional factors further reducing coral cover and contributing to macroalgal abundance were warming events in 1987, 1990 and 1998, causing large-scale bleaching and coral mortality, and changes in land use causing increased sedimentation and eutrophication. These illustrate the difficulties of distinguishing impacts of multiple causal agents acting at different temporal and spatial scales, and intensities. There is still much to be understood regarding the synergistic influence of multiple stressors, but evidence from cases of over-fishing and nutrification, suggests that in combination, these factors can incur phase shifts from coral dominated reefs to ones composed mainly of macroalgae (McCook, 1999).

In other areas of the world, recovery back to pre-disturbance levels has been quantified, and appears to be greatest following short-lived disturbances that do not physically alter the reef (Connell, 1997). Examples include recovery of coral abundance on intertidal reef flats at Heron Island, Great Barrier Reef within 10 years of disturbance by cyclones (Connell et al., 1997), recovery after 12 years following an outbreak of *Acanthaster planci* in Guam (Colgan, 1987) and recovery for 50% of their original cover only five years after a warming event in 1982-1983 in Indonesia (Brown and Suharsono, 1990). Where little or no recovery has been shown, this was attributed to patchiness in larval availability (Done, 1992). Therefore information on coral reef recovery is scarce, but where it does exist the modelled community does seem to reflect measured situations very well.

Recovery times from predictions range from 10-30 years (Wilkinson, 1999); 20-30 years (Crimp and Braddock, 1993); >50 years (Done, 1988). One reason for the reputed variability is due to differences in the criteria for recovery. Done (1988) considered recovery to be complete when the original size structure of corals within a population had returned, while others have focussed on the return of coral cover to pre-disturbance levels.

Moderate and severe warming simulations reduced total coral cover by 17% and 28% respectively. Many authors do not consider relative reductions in coral cover of less than 33% to be ecologically significant (see review by Connell, 1997), but this may simply reflect the fact that many reports of disturbance and recovery have quantified changes exclusively in coral abundance, and do not take into account other characteristics such as species composition (Connell et al., 1997). Cover was demonstrated in this study to be relatively insensitive: it may reach pre-disturbance levels in <5 years whereas community structure took at least 16 years. In conclusion, the impacts of warming, while only transiently reducing coral cover, have greater and significant ecological impacts on the coral community which last for decades.

Recovery after a moderate event was slowed by reduced coral recruitment rate, but only by 2 years or so. The greatest influences on recovery in all cases were seen following severe warming events. With reduced coral recruitment recovery time increased by 24 years, with increased algal growth, an additional 34 years, and when both these factors were applied simultaneously recovery took 90 years.

This clearly demonstrates the importance of three factors:

1) A constant supply of recruits is needed, supporting the view that supply-side ecology is fundamental to the recovery of open systems from disturbance (Lewin, 1986; Preece and Johnson, 1993).

2) Algae mediate the recovery process. In this model, algae were included as a very basic approximation. But even this approximation very successfully generated some complex behaviour, which matches observations on real reefs. A more realistic algal element might differentiate between types of algae, though this would have to be underpinned by advances in algal ecology and is not possible yet (McCook et al., 2001).

3) Reefs influenced by multiple stressors may have extremely long recovery times as such stressors can operate synergistically.

During these simulations, the variability between replicates reflects the stochastic processes of background disturbance and also recruitment to a certain extent. This explains perhaps the lack of observable effects following mild impacts. Such variability is an intrinsic property of coral communities at this small spatial scale e.g.

metres. Variability is high on a small scale but with increasing spatial scale, there is greater community predictability (Connell and Sousa, 1983; Karlson and Hurd, 1993; Levin, 1992). Coral reefs have long been viewed as temporal mosaics, with patches in differing states of succession (Grassle, 1973). So, in many ways the coral community model compares well with real coral communities and variability inherent in the model is similar to that encountered in the field. The way this variability was overcome in this study for statistical purposes was by performing a minimum of 20 replicates of each simulation; in effect this may be considered analogous to increasing plot area from 9 m^2 to 180 m^2. In the field however, areas as large as this are rarely sampled.

Chapter 7. Effects of repeated climatic impacts on the coral community

7.1. Objectives

The overall objective of this chapter is to employ the model in conjunction with predictions of future warming episodes to gain insight into how coral communities and populations are likely to change over the course of the next 100 years. Previous chapters have illustrated the capacity of the model to predict coral communities and assessed the accuracy of such predictions. Here sea surface temperature predictions from a coupled ocean atmosphere general circulation model, the most powerful tool available for constructing plausible estimates of future climate changes, are applied to the coral community model, together with species-specific thermal responses of coral species characterised in Chapter 6.

The impact of climate change on coral communities remains unknown, though this phenomenon represents a major contemporary threat to coral reefs (Wilkinson and Hodgson, 1999). Pre-1998, concern for the degradation of reef systems was focussed on effects of local agents, mostly induced by human activities, and conservation and management objectives were often direct mitigation of these activities (Hughes and Connell, 1999). In the wake of the 1998 global mortality, attention has moved to encompass this global impact of warming. But knowledge in this area is scarce, as no comprehensive system is available for predicting effects of global impacts manifest on local scales, and at present community and population responses are generalised (Bak and Meesters, 1999; Done, 1999; Hoegh-Guldberg, 1999).

Specific aims were:

1. To characterise community responses to increasing frequency and intensity of warming events in order to increase our understanding of the resilience of coral

communities to climate change. Trajectories that communities take under such stress could ultimately aid in reef management decisions.

2. To quantify changes in the size structure of coral populations. Rates of these changes in colony size may be slow and gradual, or occur in steps. Understanding responses of coral populations to climate change can yield insight into the vulnerability of individual species to intensified warming episodes, and help generate an understanding of how future reefs might be structured.

3. Investigate the influence of environmental factors acting locally that might operate synergistically with warming events to intensify the rate and pattern of decline of the coral community. Specifically these scenarios were 1) enhanced algal growth (mimicking potential reef nutrification or low grazer densities) and 2) reduced coral recruitment, simulating differing degrees of connectivity of the modelled reef.

7.2. Methods

7.2.1. Assumptions

All the assumptions in previous chapters are applied to this investigation with the following additional ones:

1. Corals do not adapt or acclimatize to temperature change at the speed needed to respond to current trends. This is an active topic of research and was discussed in the Introduction, Section 1.5.5.

2. Sea surface temperatures (SSTs) correlate to sub-surface sea temperatures which bathe the corals. This is unlikely to consistently be the case, but there are few long-term data sets of subsurface sea temperature available, and this assumption is regularly made when using SST based data to infer bleaching (Quinn and Kojis, 1999).

3. Bleaching is induced solely by high sea temperatures. Although solar radiation has been implicated as an important factor (Fitt et al., 2001), it is not included here because of lack of predictions of light levels.

4. The bleaching history of individual coral colonies has no influence on its vulnerability in future warming events[9].

5. Climate change is manifest solely as increased SST. Aragonite saturation level (Kleypas et al., 1999), storm frequency/intensity changes (Pittock, 1999) and sea level rise (Done, 1999) are also likely to change with climate, but are not included here for reasons as above.

7.2.2. HadCM3GGa

To obtain an indication of the frequency and intensity of future warming events, the Hadley Centre's third generation coupled ocean atmosphere general circulation model (HadCM3) data were used. This global climate model was chosen on the basis of its low drift over long periods, and that it is the first in a new generation of models not to require flux adjustments. Characteristics of the model are given in Appendix 4. From the various model integrations, the greenhouse gas (GGa1) data were used for this work. HadCM3GGa1 was forced using the historical increase in individual greenhouse gases (GHGs) from 1860-1990, and then using individual increases in GHGs as described in the IS95a (a 1% per year compound rise in radiative forcing) emissions scenario (IPCC, 1992; IPCC, 1996)[10].

7.2.3. Applying HadCM3 predictions to the coral community model

7.2.3.1. Site selection

Belize was chosen as the site simulated by the model (Figure 7.1) because there are several bleaching reports from this area (thus the parameter values are partly based on the response of Belizean coral communities to warming), and climatic details are

[9] Since this work was done, (Brown et al., 2002) have found that history is an important factor in the bleaching responses of corals in Phuket.

[10] HadCM3 integrations with SRES emissions scenarios (IPCC, 2001) could not be used in this study, as these had not been run with HadCM3 at the time of this work.

known[11]. Also field measurements of coral competition were from this region (see Section 3.2.2)

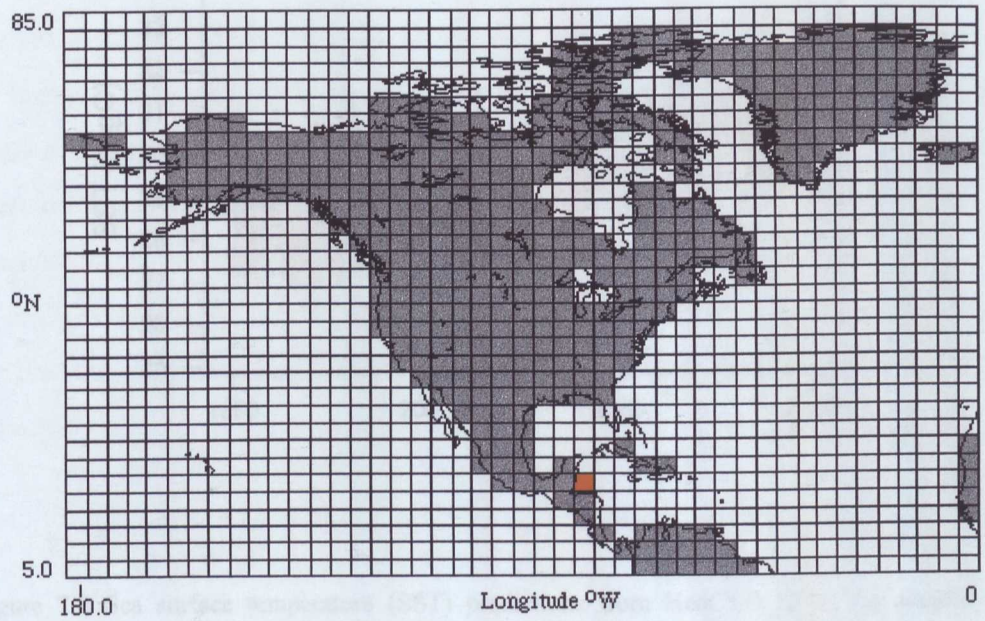


Figure 7.1 Map of HadCM3 grid coordinates, with location of Belize subsample indicated in red (83°30' – 87°15'W, 15°00' – 17°50'N).

HadCM3 predictions for Belize show trends of increasing sea surface temperature over the next 100 years. This increase accelerates during the second half of the 21st century (Figure 7.2).

[11] http://orbit-net.nesdis.noaa.gov/orad/sub/sst_series_24reefs.html

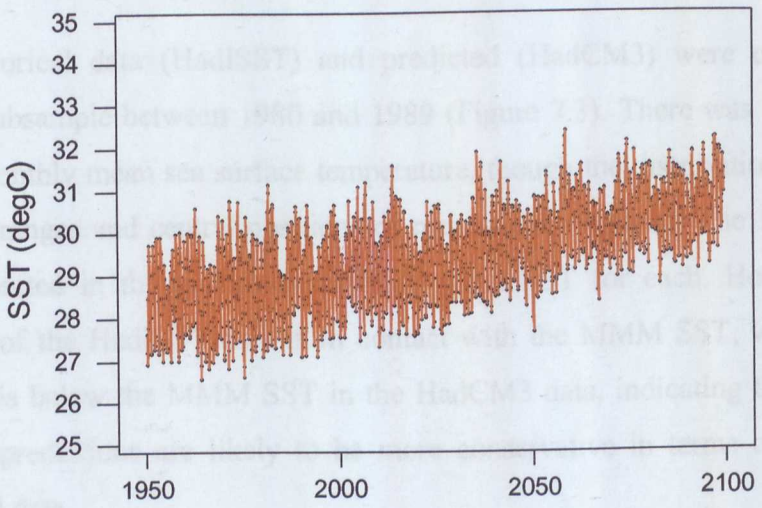


Figure 7.2 Sea surface temperature (SST) predictions from HadCM3_GGa1 (as monthly means) plotted for Belize (83°30' – 87°15'W, 15°00' – 17°50'N) between 1950 and 2099.

7.2.3.2. Accuracy assessment

In order to check the accuracy of the HadCM3 predictions for the Belize subsample, and confirm the position of known thresholds of coral thermal tolerance, these data were compared to historical data, HadISST. This is a monthly global SST and sea ice data set from a combination of *in situ* sea surface observations (ship tracks) and satellite-derived estimates, with gaps filled using an empirical orthogonal function technique. Annual mean SST climatology from HadISST and other climatologies are in agreement over most regions of the globe to within a few tenths of a degree centigrade, and have been validated for reef areas with widely ranging temperatures (Sheppard and Rayner, 2002).

The maximum monthly mean (MMM) SST was calculated for a 20 year period between 1980 and 1999 for the Belize subsample from the HadCM3 data, and found

to be 30 °C. This is 1.1°C higher than Glovers Atoll, Belize (28.9 °C, documented by NOAA)[12].

The historical data (HadISST) and predicted (HadCM3) were compared for the Belize subsample between 1980 and 1989 (Figure 7.3). There was a 1 °C difference in the monthly mean sea surface temperature, though the distributions of the data are similar (ranges and central positions of means and medians). The 1 °C difference is also reflected in the maximum monthly mean SST for each. However, the upper quartile of the HadISST data is in contact with the MMM SST, whereas the upper quartile is below the MMM SST in the HadCM3 data, indicating that the HadCM3-derived predictions are likely to be more conservative in terms of anomalies than observed data.

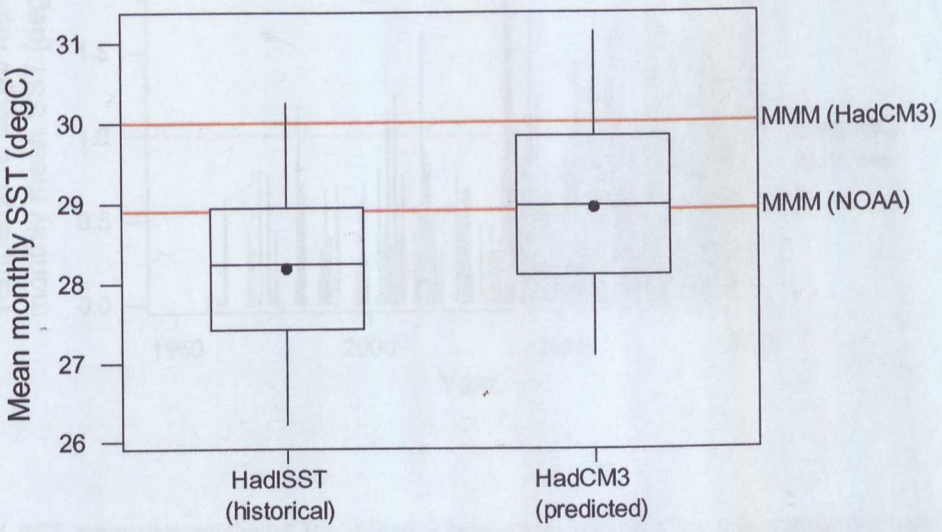


Figure 7.3 Mean monthly sea surface temperature (SST) data between 1980 and 1989 plotted for HadISST dataset (historical) and HadCM3 (predicted) for Belize. Boxes indicate quartiles and the circles indicate means. MMM indicates maximum monthly mean SST.

7.2.3.3. Extraction of degree heating months

SST anomalies were calculated by subtracting HadCM3 predicted SSTs from the derived MMM SST (Figure 7.4). This identified the magnitude of warming events predicted by HadCM3 but did not take into account their duration, a factor that can

[12] http://www.osdpd.noaa.gov/PSB/EPS/SST/dhw_news.html

have considerable influence on the severity of the effect (Williams and Bunkley-Williams, 1988). Therefore degree heating months (DHM) were calculated (Figure 7.5); 1 DHM is equivalent to the monthly mean SST being 1°C above the MMM SST, 2 DHMs can either be two consecutive monthly means 1°C above the MMM SST or 1 month 2°C above the MMM. Warming events of 10+ degree heating weeks have been observed to cause severe bleaching and often mortality, (~2.5 DHM)[13]. The upper threshold for 'mild' warming events was set at 1 DHM, and 'moderate' warming events at 3 DHM, and everything above this is considered 'severe' (and to date not experienced in the Western Atlantic region).

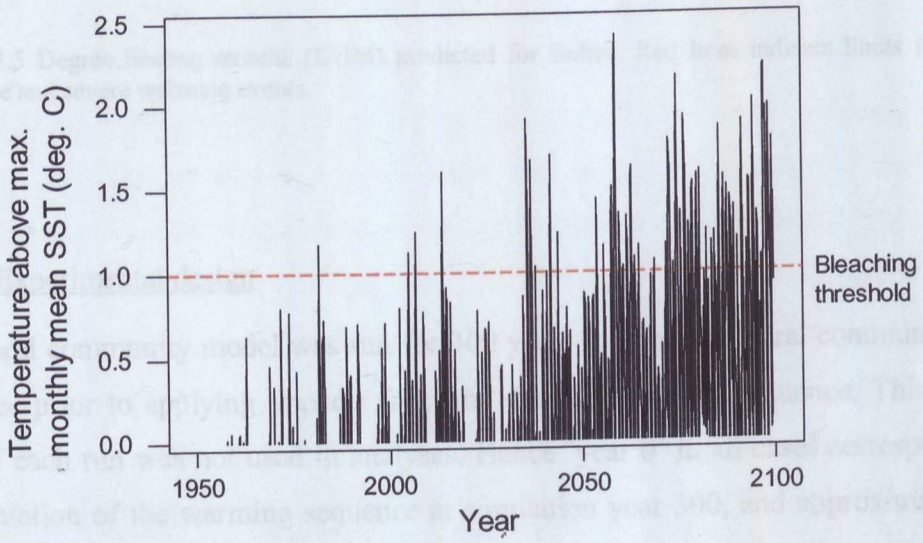


Figure 7.4 SST anomalies predicted for Belize. These were calculated by subtracting the maximum monthly mean (MMM) SST from HadCM3 predicted SSTs. The threshold for coral bleaching is indicated (1°C above MMM).

[13] http://www.osdpd.noaa.gov/PSB/EPS/method.html

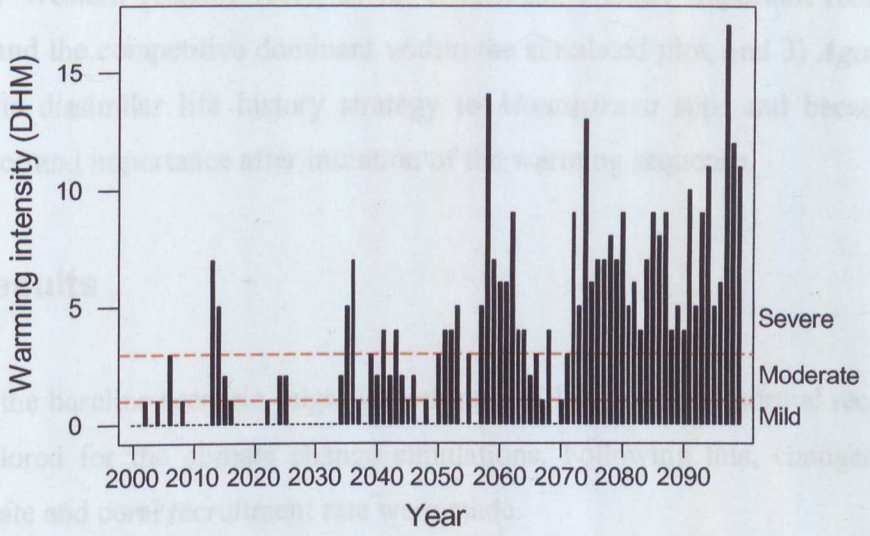


Figure 7.5 Degree heating months (DHM) predicted for Belize. Red lines indicate limits for mild, moderate and severe warming events.

7.2.4. Experimental design

The coral community model was run for 300 years to allow the coral communities to stabilize prior to applying impacts from the derived warming sequence. This initial part of each run was not used in analyses. Hence 'year 0' in all cases corresponds to the initiation of the warming sequence at simulation year 300, and approximates the year 2000. 20 replicates were made for four scenarios (for more detail, see Chapter 6, Section 6.2.4 and Figure 6.3), and the results were taken as percent cover, (every year), and number and size of coral colonies (at 10 year intervals between 0 and 90 years).

7.2.4.1. Population structure analysis

Colonies from the 20 replicates were pooled for broad size classes on a log scale, and the proportion in each size class calculated by species for each time increment. For the baseline scenario, the dynamics of all coral species were examined.

To assess the influence of the different scenarios with increasing frequency and intensity of warming events, the dynamics of three key coral species were compared. These were: 1) *M. annularis*, which is the dominant reef-framework building species

on many Western Atlantic reefs, 2) *M. cavernosa*, another important reef-building species and the competitive dominant within the simulated plot, and 3) *Agaricia* spp. due to its dissimilar life history strategy to *Montastraea* spp. and because of its abundance and importance after initiation of the warming sequence.

7.3. Results

Initially the baseline scenario (algal growth rate of 1 cm yr^{-1} and normal recruitment) was explored for the climate change simulations. Following this, changes to algal growth rate and coral recruitment rate were made.

7.3.1. Community dynamics

Following the application of the warming sequence, the community rapidly lost its integrity, and shortly after 10 years there was an unprecedented decline in the abundance of *Montastraea annularis* (the spatially dominant species) (Figure 7.6). Following each subsequent warming event, algal abundance increased, and after a 3-6 year lag, a peak in *Agaricia* spp. was visible. Some species did not recover at all, such as *M. annularis*, which was more or less absent from 15 years onwards, while others showed a slower decline, e.g. *M. cavernosa* and *Porites astreoides*. *Madracis* spp. increased in abundance from around 1% to 30%. Other bleaching tolerant species, such as *Eusmilia fastigiata* and *Meandrina meandrites* were also able to persist in the highly disturbed environment.

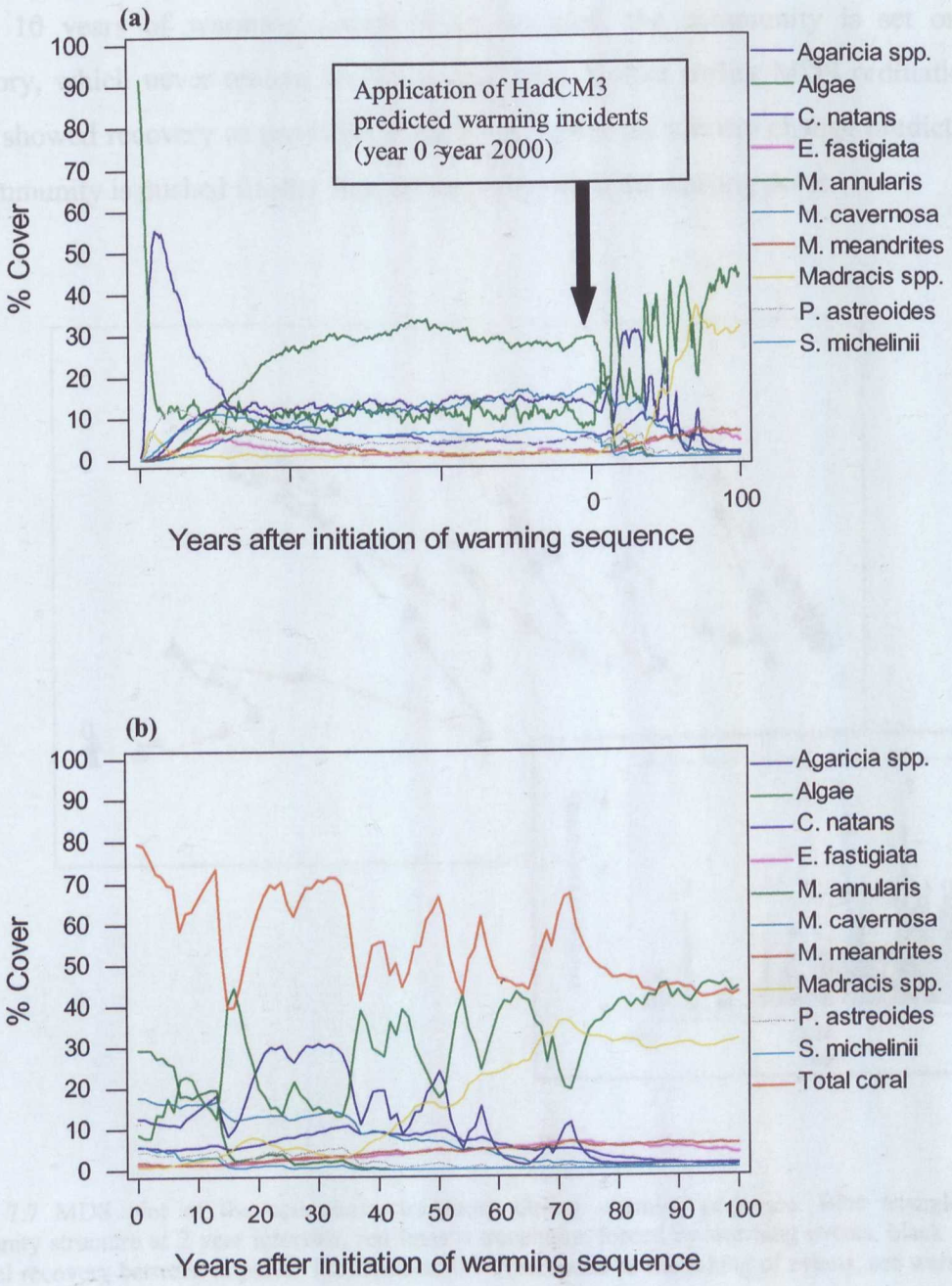


Figure 7.6 Corals community dynamics with predicted climate change. (a) Output from entire simulation, (b) Community response to warming sequence. Percent cover, mean of 20 replicates.

Breakdown of community integrity is evident from the MDS plot (Figure 7.7), where the main trend of decline runs from left to right, but is complicated by the diagonal pattern of disturbance and recovery. Disturbance is characterised by peaks in algal

abundance immediately following warming events and initial recovery processes are predominately characterised by increases in *Agaricia* spp. Also it is apparent that within 10 years of warming events being initiated, the community is set on a trajectory, which never returns to its starting state. Unlike earlier MDS ordinations which showed recovery to pre-impact condition, under the climate change prediction the community is pushed further and further away from the starting point.

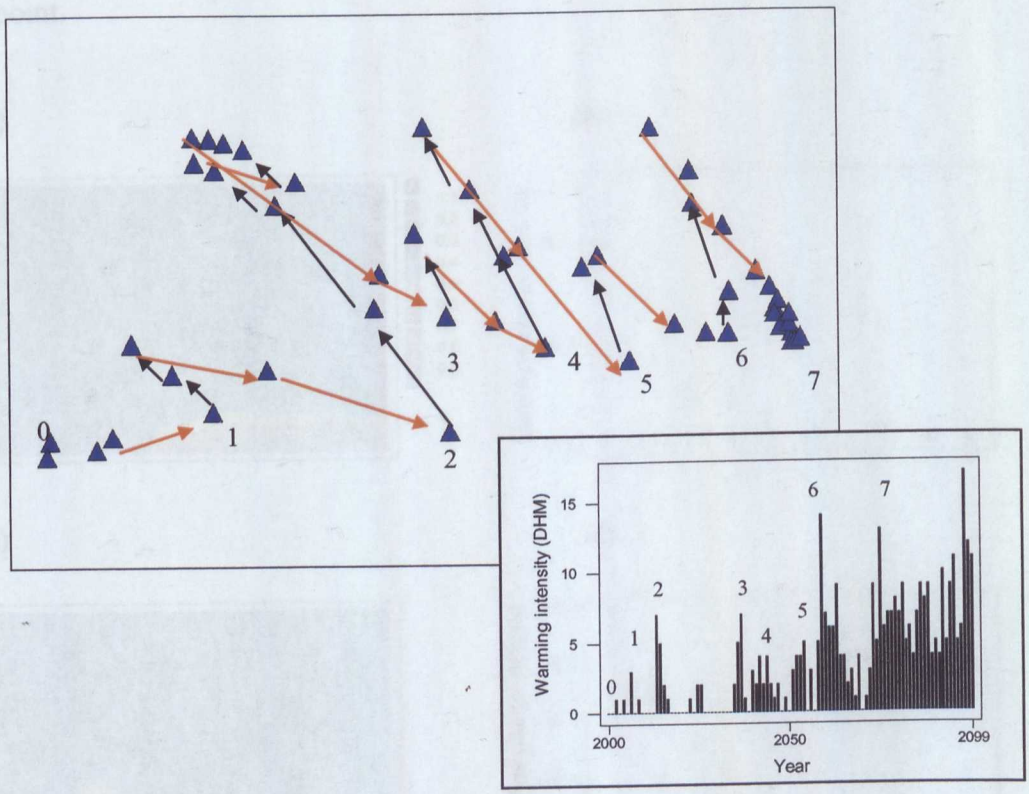


Figure 7.7 MDS plot of the community trajectory during warming sequence. Blue triangles = community structure at 2 year intervals, red lines = transitions forced by warming events, black lines = partial recovery between impacts. The numbers 0-7 correspond to the timing of events, see warming sequence insert.

7.3.2. Population dynamics

The size structure of coral populations underwent changes with increasing intensity and severity of warming incidents. Coral species were categorised according to their dynamics: 1) rapid decline with the onset of warming events, 2) gradual decline, 3) initial increase then subsequent decline, 4) gradual increase.

7.3.2.1. Species exhibiting a rapid decline

Two species fell into this category: *Montastraea annularis and Stephanocoenia michelinii* (Figure 7.8). In the case of *M. annularis*, the steep decline was complete at 20 years (simulating the year 2020). At this point the population of *M. annularis* was almost non-existent (though there is some sporadic recruitment). This is reflected both in the population size structure and the number of colonies (Figure 7.8). In *S. michelinii,* the decline was complete by 40 years, though small corals were present after this point.

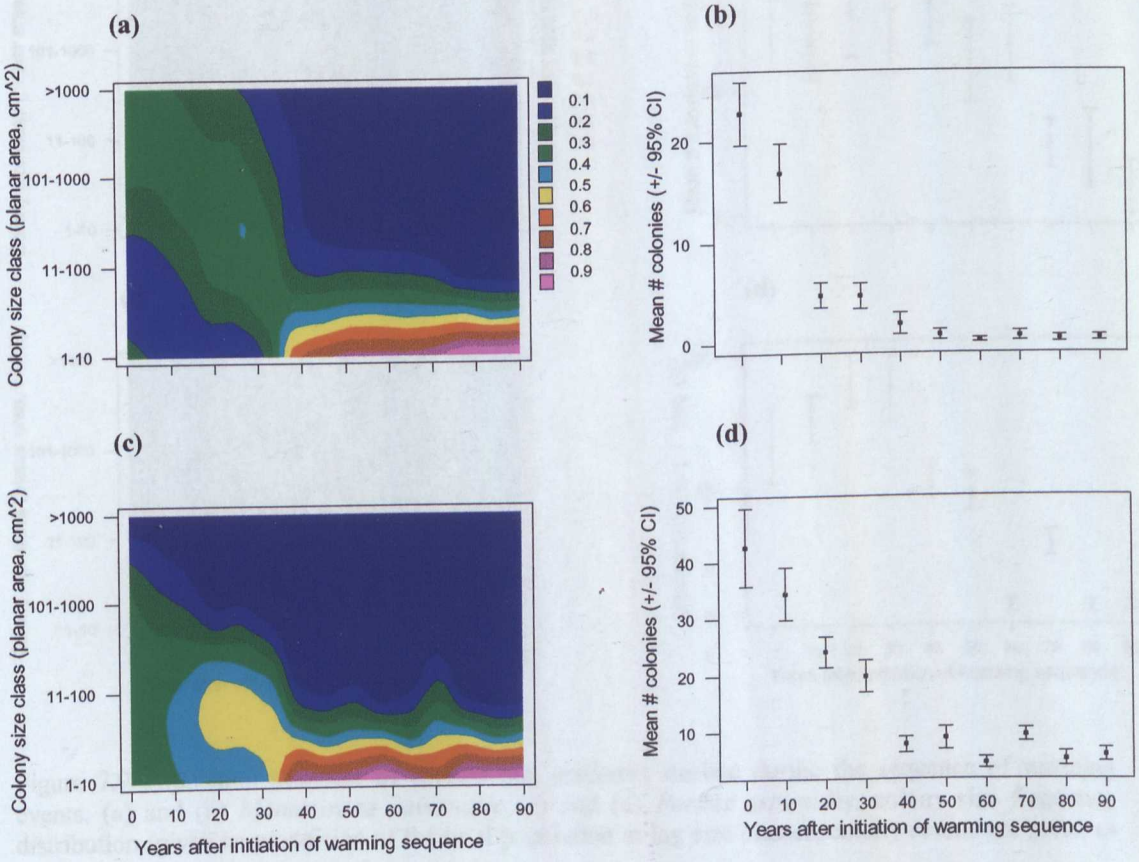


Figure 7.8 Population structures of species that rapidly decline during the sequence of warming events. (a) and (b) *Montastraea annularis*, (c) and (d) *Stephanocoenia michelinii*, colony size frequency distribution (given as proportion of the total population in log size classes) and colony counts (given as mean ± 1SD, n = 20) respectively.

7.3.2.2. Species that gradually declined

Montastraea cavernosa and *Porites astreoides* both showed a gradual decline in size structure and colony counts (Figure 7.9). In both cases, the size decrease was strongly linear, while number of colonies decreased slowly initially but then dropped off rapidly in *M. cavernosa*. In *P. astreoides*, the number of colonies initially increased, only declining 30 years into the warming sequence.

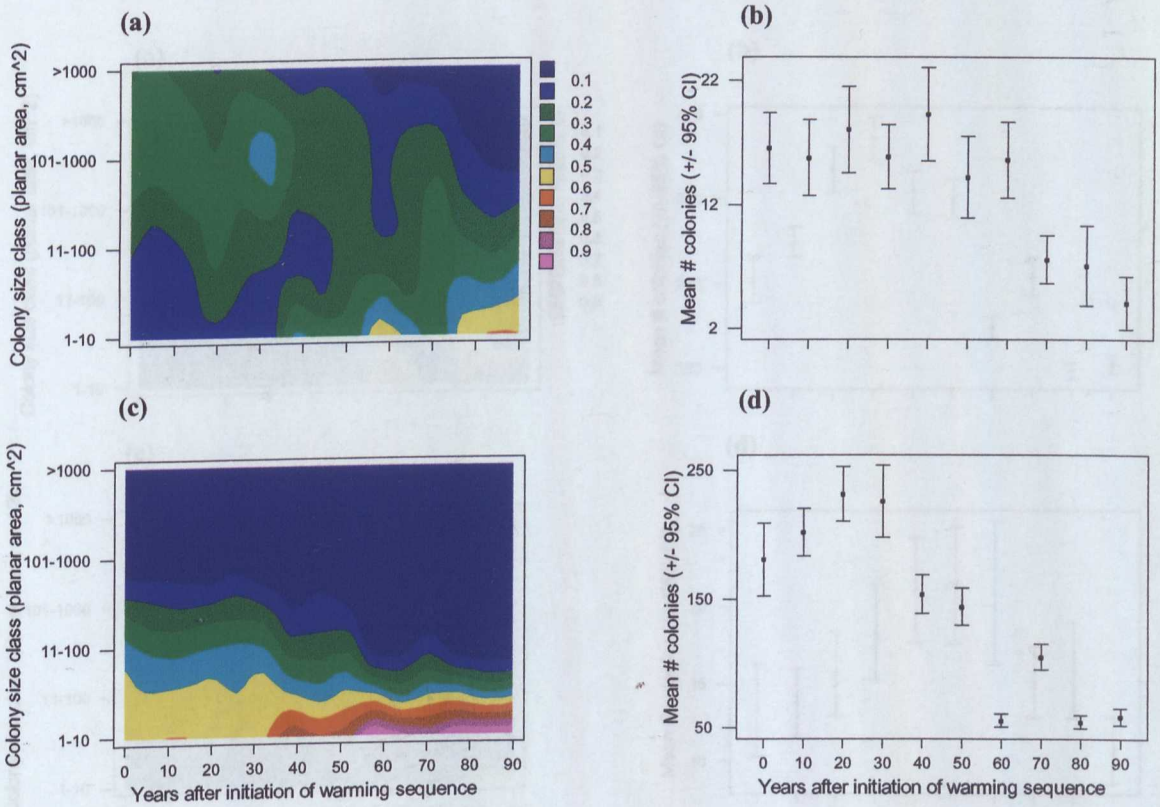


Figure 7.9 Population structure of species that gradually decline during the sequence of warming events. (a) and (b) *Montastraea cavernosa*, (c) and (d) *Porites astreoides*, colony size frequency distribution (given as proportion of the total population in log size classes, colony counts are given as mean ± 1SD, n = 20), respectively.

7.3.2.3. Species that initially increased then declined

Agaricia spp. and *Colpophyllia natans* both increased in population size structure and number as the sequence of warming events commenced (Figure 7.10). 40 years into the warming sequence though, both species underwent a decline in both attributes.

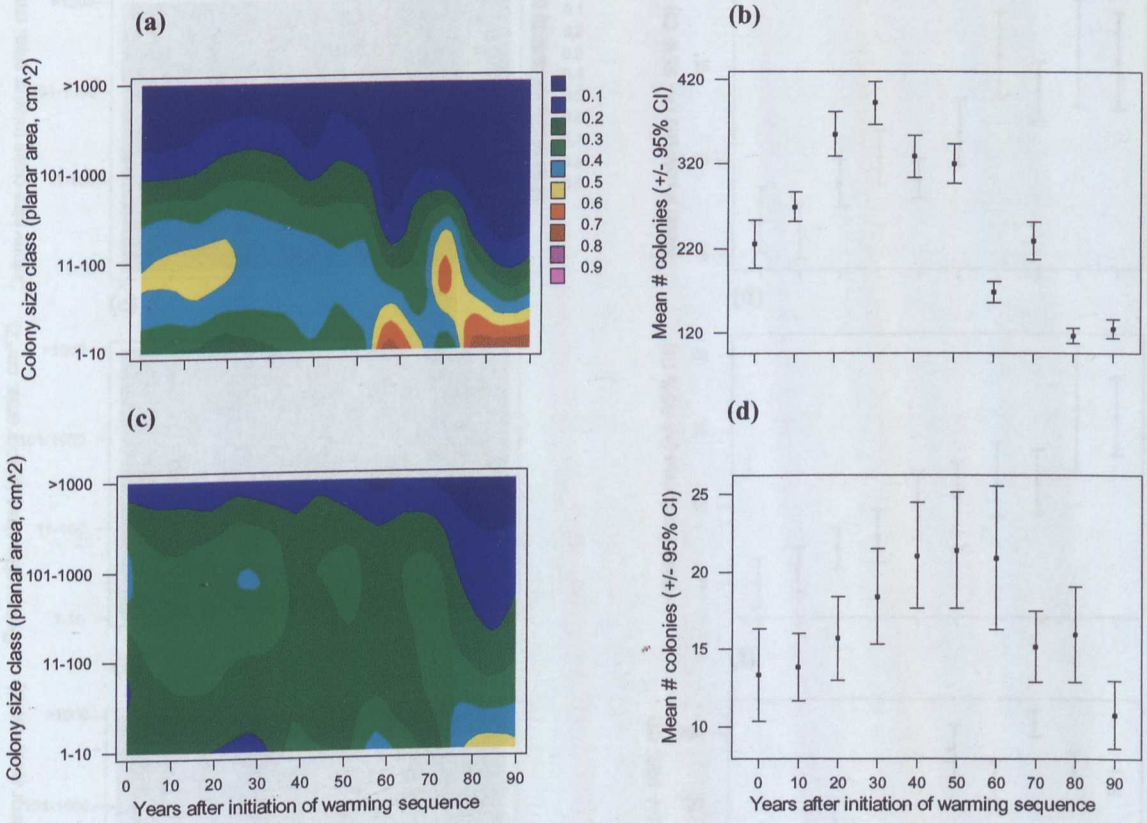


Figure 7.10 Population structure of species that initially increase and subsequently decline during the sequence of warming events. (a) and (b) *Agaricia* spp., (c) and (d) *Colpophyllia natans* colony size frequency distribution (given as proportion of the total population in log size classes) and colony counts given as mean ± 1SD, n = 20) respectively.

7.3.2.4. Species that increased

The populations of the remaining three species, *Eusmilia fastigiata, Meandrina meandrites* and *Madracis* spp., increased with the sequence of warming events (Figure 7.11). *Madracis* spp. increased the most, from 32.2 ± 13.6 colonies per 9 m^2 at the start of the warming sequence to 164.8 ± 18.45 colonies per 9 m^2 at the end of the simulation, > 5-fold increase. Reasons for this are discussed later.

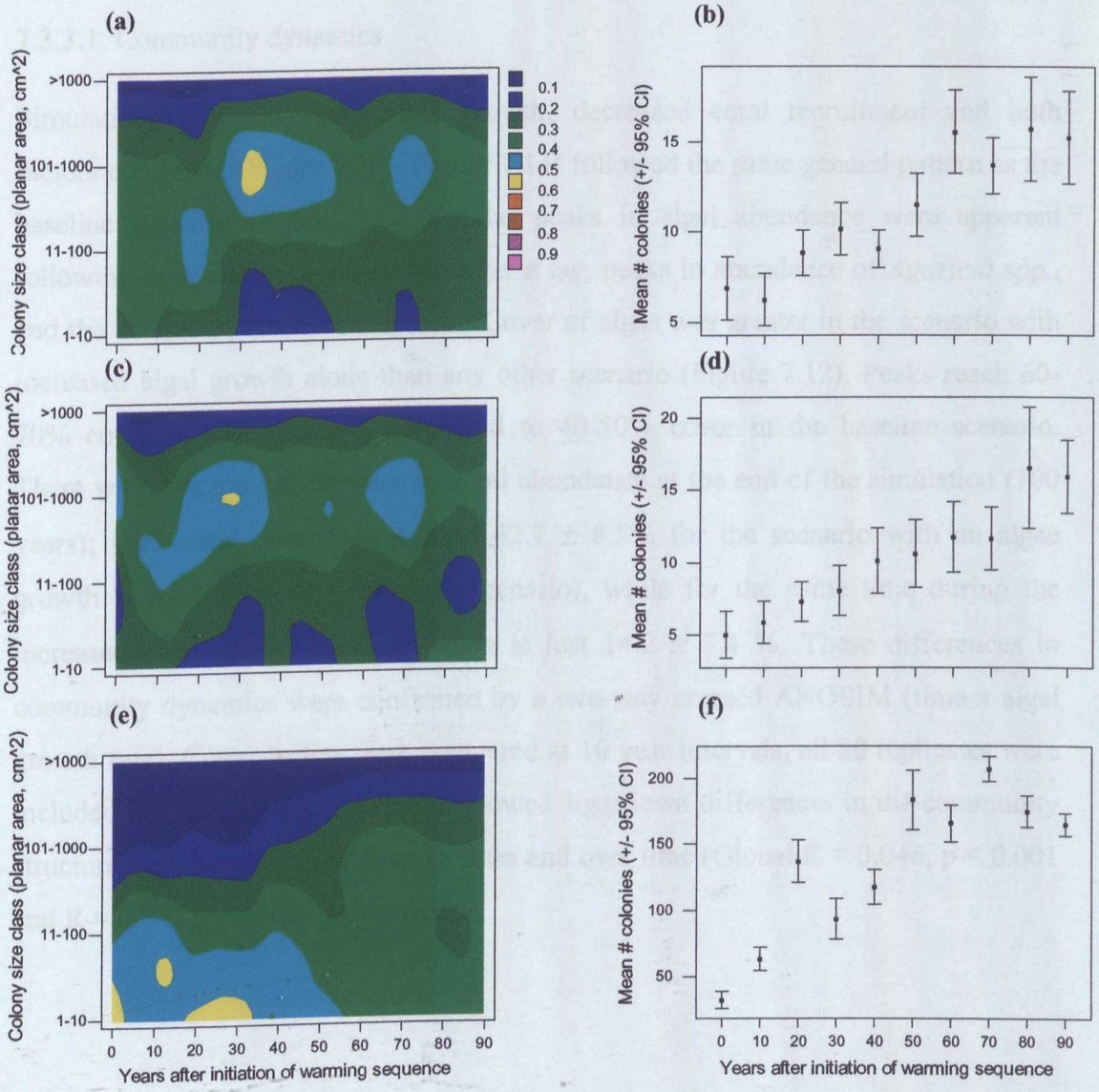


Figure 7.11 Population structure of species that increase during the sequence of warming events. (a) and (b) *Eusmilia fastigiata*, (c) and (d) *Meandrina meandrites* and (e) and (f) *Madracis* spp. colony size frequency distribution (given as proportion of the total population in log size classes) and colony counts given as mean ± 1SD, n = 20) respectively.

7.3.3. Effect of increased algal growth and decreased coral recruitment

The scenarios with different conditions of algal growth and coral recruitment, which were investigated during the single impact work (Chapter 6, Section 6.2.4.1) were also run with the warming sequence. These simulated a plot with increased algal growth rate (4 cm yr^{-1} compared with 1 cm yr^{-1}), a plot with reduced coral recruitment rates during warming events and with both factors combined.

7.3.3.1. Community dynamics

Simulations with increased algal growth, decreased coral recruitment and both factors combined (Figure 7.12 - Figure 7.14) followed the same general pattern as the baseline scenario (Figure 7.6). Similar peaks in algal abundance were apparent following each warming event, and after a lag, peaks in abundance of *Agaricia* spp., and the decline of most coral species. Cover of algae was greater in the scenario with increased algal growth alone than any other scenario (Figure 7.12). Peaks reach 60-70% cover in this scenario, compared to 40-50% cover in the baseline scenario. There was a reciprocal decrease in coral abundance at the end of the simulation (100 years); total coral cover was around 42.7 ± 8.5% for the scenario with an algae growth rate of 1 cm yr^{-1} (baseline scenario), while for the same time during the increased algal growth scenario, there is just 14.2 ± 3.4 %. These differences in community dynamics were confirmed by a two-way crossed ANOSIM (time x algal growth rate). Communities were compared at 10 year intervals, all 20 replicates were included in the analysis, and results showed significant differences in the community structure both between algal growth rates and over time (Global $R = 0.046$, $p < 0.001$ and $R = 0.742$, $p < 0.001$ respectively).

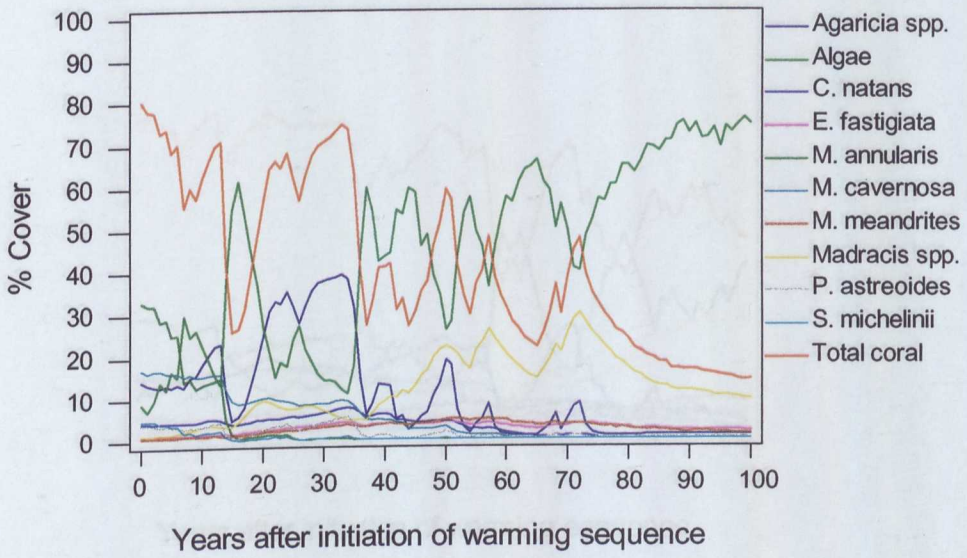


Figure 7.12 Effect of increased algal growth on modelled coral community. Percent cover of coral community following repeated warming events between 0 years (~ year 2000) and 100 years (~ year 2100), mean of 20 replicates.

Reduced recruitment did not cause the same strong peaks in abundance of *Agaricia* spp. as seen during the baseline scenario (Figure 7.13 and Figure 7.1 respectively). Interestingly, total coral cover generally appears higher within this scenario, and decreases in coral cover immediately following a warming event seem to be less than when recruitment rates are unchanged. These differences in community structure were significant when a two-way crossed ANOSIM (recruitment scenario x time) was carried out on the data (at 10 year intervals, using 20 replicates), (Global $R = 0.397$, $p < 0.001$, global $R = 0.678$, $p < 0.001$, for recruitment scenario and time interval respectively).

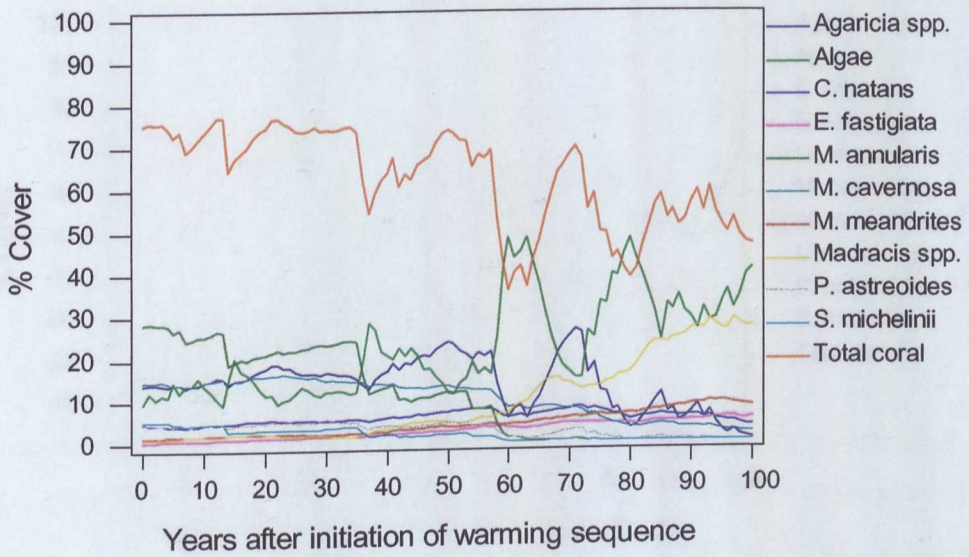


Figure 7.13 Effect of reduced coral recruitment on modelled coral community. Percent cover of coral community following repeated warming events between 0 years (~ year 2000) and 100 years (~ year 2100), mean of 20 replicates.

The combined effect of increased algal growth and reduced coral recruitment (Figure 7.14) was similar to that with reduced recruitment only (Figure 7.13). Corals declined in a similar manner, but the main difference lies in the abundance of algae, which is nearly 50% greater in the simulation with increased algal growth rate (Figure 7.14).

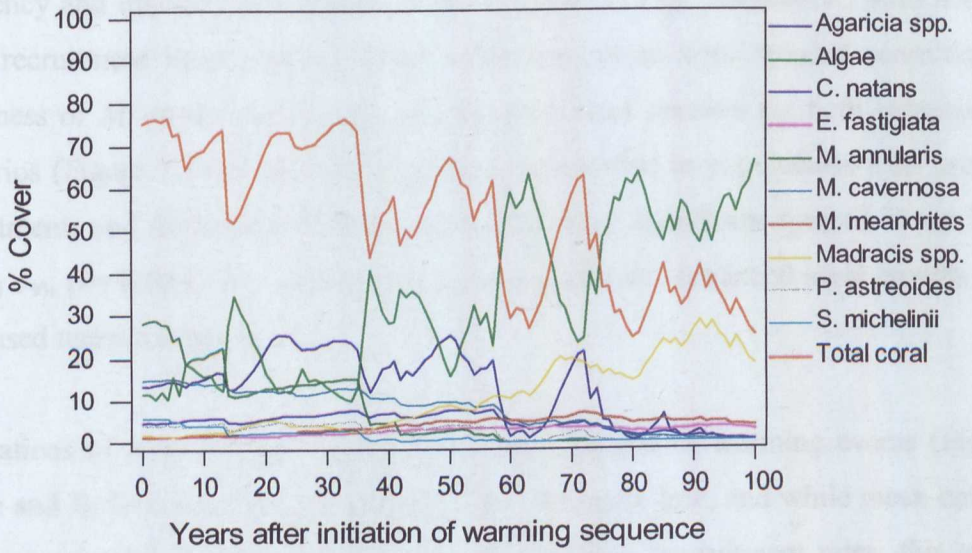


Figure 7.14 Combined effect of increased algal growth and reduced coral recruitment on modelled coral community. Percent cover of coral community following repeated warming events between 0 years (~ year 2000) and 100 years (~ year 2100), mean of 20 replicates.

7.3.3.2. Population dynamics

Populations of *Montastraea annularis* show clear differences over time between the four scenarios. Firstly, there is a difference in mean colony size between the model runs with enhanced algal growth and those with an algal growth rate of 1 cm $year^{-1}$. The former had consistently smaller colonies, indicating that algal growth mediates size of *M. annularis* colonies (Figure 7.15a).

Secondly, there are differences in both mean colony size and skewness of log-transformed populations between scenarios with normal and reduced coral recruitment (Figure 7.15 a and b). With reduced recruitment, mean colony size was larger as small colonies killed during events were not replaced, leaving a non-fecund, relict population. This is reflected in the skewness, which under conditions of normal recruitment, became more positive (shifted towards smaller colony size classes) with the initiation of the warming sequence, but with reduced recruitment remained negative, although differences were not significant (paired T-test, $T = 1.55_{(df = 4)}$, $p = 0.196$). Kurtosis however, appears not to be affected.

Montastraea cavernosa declined more gradually than *M. annularis* with increasing frequency and intensity of warming events (Figure 7.15 c). Simulations with normal coral recruitment have smaller colony sizes than those with reduced recruitment. Skewness of *M. cavernosa* populations becomes more positive for both recruitment scenarios (Figure 7.15 d), but this effect was intensified in populations with normal recruitment, and differences between scenarios were significant (paired T-test $T = 3.91_{(df = 9)}$, $p = 0.004$). As with *M. annularis* populations, enhanced algal growth rate decreased mean colony size.

Populations of *Agaricia* spp. closely tracked the profile of warming events (Figure 7.15 e and f). Size variability of colonies was extremely low, and while mean colony size was generally greater under regimes with reduced recruitment rates, this trend was only apparent towards the end of the simulations (> 50 years). Like *Montastraea annularis* and *M. cavernosa* populations, skewness increased over the course of warming events, but was not significantly different between the two recruitment scenarios (paired T-test, $T = 0.89_{(df = 9)}$, $p = 3.98$). Skewness of coral population sizes appeared to be sensitive to warming events, at 60 and 80 years there are positive shifts (i.e. towards smaller size classes), which coincide directly with severe warming events (Figure 7.5 f). Unlike the other two species, algal growth rate did not appear to influence the size of colonies.

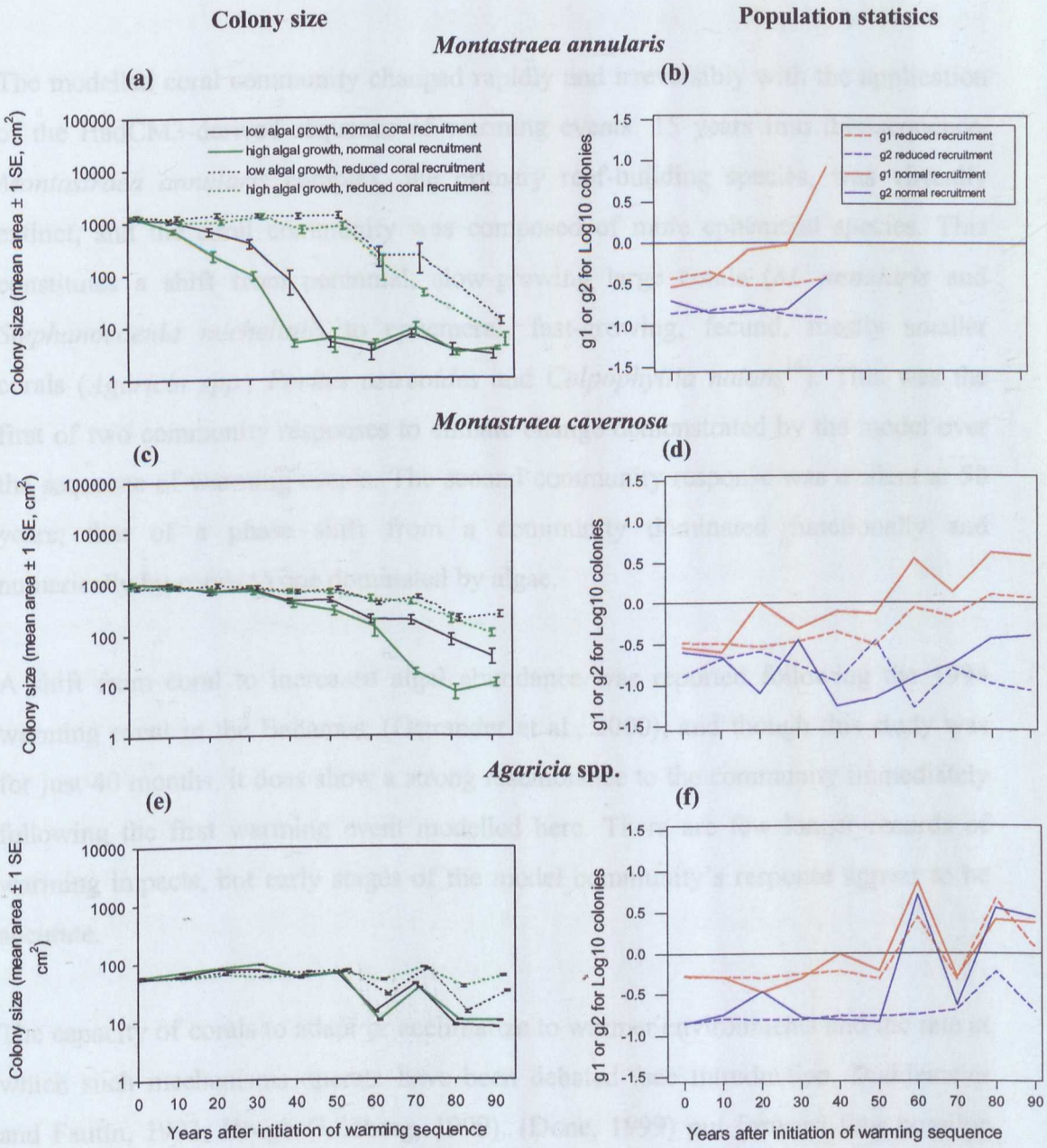


Figure 7.15 (a) and (b) *Montastraea annularis*, (c) and (d) *M. cavernosa*, (d) and (e) *Agaricia* spp. (a), (c) and (e) show mean colony size for all scenarios, while (b), (d) and (f) compare population statistics (g1 = skewness, g2 = kurtosis) for log-transformed populations between scenarios with normal and reduced coral recruitment. N = 20 replicates per scenario. Population statistics are only shown for *Montastraea annularis* for the first 40 years of the warming sequence, as after this point sample sizes became very small, as the populations were virtually extinct.

7.4. Discussion

The modelled coral community changed rapidly and irreversibly with the application of the HadCM3-derived sequence of warming events. 15 years into this sequence, *Montastraea annularis* complex, the primary reef-building species, was virtually extinct, and the coral community was composed of more ephemeral species. This constitutes a shift from perennial, slow-growing large corals (*M. annularis* and *Stephanocoenia michelinii*) to ephemeral, fast-growing, fecund, mostly smaller corals (*Agaricia spp., Porites astreoides* and *Colpophyllia natans*[14]). This was the first of two community responses to climate change demonstrated by the model over the sequence of warming events. The second community response was evident at 50 years; that of a phase shift from a community dominated functionally and numerically by corals to one dominated by algae.

A shift from coral to increased algal abundance was reported following the 1994 warming event in the Bahamas, (Ostrander et al., 2000), and though this study was for just 40 months, it does show a strong resemblance to the community immediately following the first warming event modelled here. There are few longer records of warming impacts, but early stages of the model community's response appear to be accurate.

The capacity of corals to adapt or acclimatize to warmer environments and the rate at which such mechanisms operate have been debated (see Introduction, Buddemeier and Fautin, 1993; Hoegh-Guldberg, 1999). (Done, 1999) put forward four possible community responses: tolerance, faster turnover, strategy shift and phase shift. This study has demonstrated the latter two responses. For the community to respond with a faster turnover of populations of the same species, it is assumed that coral reefs experience increases in mortality that reduce life expectancy; thus the same species shift to a younger age structure. This response was observed to a certain extent in the modelled community for three species.

[14] This is generally not a small species, but shares life history attributes such as high rates of growth and reproduction with small species so is included here for this reason.

The timing of these community responses may be conservative. Using data from several GCMs (ECHAM4/OPYC IS92a, ECHAM3/LSG IS92a, CSIRO DAR), Hoegh-Guldberg (1999) predicted that Caribbean reef systems will be experiencing near-annual bleaching events that exceed the extent of the 1998 bleaching event by the year 2020. The warming sequence derived from HadCM3 data is more conservative than this, with near-annual events occurring from the year 2035, thus depending on which GCM is applied and the thermal tolerance threshold of corals used, SST anomaly predictions can greatly vary.

Life history strategy and variation in vulnerability to mortality during warming events means that Caribbean coral species were differentially affected. While some species appeared initially quite resistant to repeated impacts, e.g. *Agaricia* spp. others such as *M. annularis* and *S. michelinii* were extremely vulnerable. Within 15 and 30 years of warming sequence initiation, populations of *M. annularis* and *S. michelinii* declined to near extinction, with no evident recovery. This is explained by the fact that these species are relatively slow growing. Also *M. annularis* has an extremely low rate of recruitment (Bak and Engel, 1979; Rylaarsdam, 1983). Previous matrix modelling studies have shown that stable populations of *M. annularis* can be maintained without larval input, solely by fragmentation of existing colonies (Hughes and Tanner, 2000). *M. annularis* and *S. michelinii* are also highly vulnerable to bleaching (Lang et al., 1988; Meesters and Bak, 1993; Wilkinson and Hodgson, 1999). This combination meant that once the populations were impacted during a warming event early in the sequence, recovery was so slow as to be rendered undetectable and subsequent impacts further depleted them. At the beginning of the warming sequence, the 95 percentile colony size for *M. annularis* was 5382 cm^2 planar area i.e. approximate radius 41.4 cm. So, assuming a growth rate of 1 cm yr^{-1}, it would take at least 42 years for the largest colonies to be replaced if they were killed. However, the longest period between subsequent events was eight years, illustrating the differences in required recovery time and predicted repeated warming events.

Dramatic declines in *M. annularis* populations have been documented in Jamaica in the mid 1980s, caused by impacts from hurricane damage and the results of the die-off of an echinoid grazer, *Diadema antillarum* (Hughes and Tanner, 2000). A

dramatic shift in the size of colonies occurred between 1987 and 1993, with almost all large colonies dismembered into small remnants, which have a higher mortality rate than large corals (see Introduction). Many were subsequently overgrown by algae.

When different scenarios of algal growth and coral recruitment were compared, it is apparent that reduced recruitment rate had a marked effect on the mean size of *M. annularis* colonies. This is likely to be a result of two factors:

1. The mean size of colonies is maintained at pre-disturbance levels due to the lack of small colonies. Small colonies have a higher mortality rate than large ones, thus are more likely to be killed during warming events or during background mortality processes. If recruitment is low then these colonies are not replaced, so even if the largest colonies are lost from the population by fragmentation, the mean size of *M. annularis* remains high. This is supported by the comparatively negative skewness of log-transformed size frequency distributions for populations with reduced recruitment relative to the more positive distributions from populations with normal recruitment (a trend seen in two other species as well, but only found to be significant in *M. cavernosa* populations). However, a general trend in increasingly positive skewness indicates an overall population shift to small size classes, supporting the hypothesis proposed by Done (1987).

2. An alternative theory is related to the density dependence of *M. annularis* colony sizes (see Chapter 4). Within the model, a relationship exists between recruitment rate and colony size. It is possible that the decrease in recruitment elicited a response in the surviving colonies to grow into all available space, and as recruitment was low, intraspecific spatial competition was also low.

The vulnerability of *M. annularis* demonstrated by the model may even be underestimated, due to two further mechanisms enhanced by its life history strategy (in particular its low fecundity, propensity for asexual reproduction and longevity): Firstly, the Allee effect, (inverse density dependence at low density), which would mean chronic reproductive failure (Courchamp et al., 1999; Knowlton, 2001). Secondly, in the event that adaptation is possible for corals within the scale of

climate change (see Introduction, Section 1.5.5), *M. annularis* is not best equipped to adapt as a) due to its extreme clonality, many colonies on a reef share the same genotype and are likely to be equally impacted, and reproducing mostly asexually means there is not much opportunity for genetic recombination to generate adaptive traits (Lasker and Coffroth, 1999), b) long generation times mean a low turnover of adaptive traits, and c) as colonies shift to smaller sizes with the fragmentation of large colonies, they may no longer be fecund (Szmant, 1986), (reproductive size is correlated with colony size of the species, Soong, 1993, and *M. annularis* forms large colonies, Meesters et al., 2001) thus increasing influence of the other effects. Although this is probably true of all corals, it is likely to be particular significance for *M. annularis.*

Species that declined slowly had different mechanisms to maintain their population structures. *Montastraea cavernosa* is reasonably resistant to bleaching during warming events, while *Porites astreoides* is moderately susceptible to it, but has a high recruitment rate and is relatively short-lived. Because of these characteristics, these species declined slowly. The capacity of *P. astreoides* to resist disturbances in Belize following bleaching and a strong hurricane in 1998, was demonstrated by an increase in density by 9%, leading the author to conclude that these disturbances actually benefited the population (M. D. McField, pers. comm.).

Agarica spp. and *Colpophyllia natans* increased after initiation of the warming sequence, before declining. *Agaricia* spp. populations nearly doubled their original number by year 30 before declining to about half their original number. This is due to the opportunistic life history of this species. As space within the plot became available with the rapid decline of *M. annularis* and *S. michelinii*, survival of juvenile Agariciids increased. Although this species is susceptible to bleaching, the opportunity for population expansion appeared to outweigh the impacts of climate change, at least for the first part of the warming sequence. Transition matrix modelling of *Agaricia agaricites* under different regimes of hurricane disturbance found it to be highly resilient, at constant high rates of recruitment (Andres and Rodenhouse, 1993).

Under the scenario with decreased coral recruitment, simulating a plot located on a reef with low connectivity (and/or high larval residence), there was no early increase in *Agaricia* spp. This demonstrates how dynamics are tightly controlled by the availability of recruits. *Agaricia spp.* have been characterised as brooders (i.e. release planula larvae) (Szmant, 1986), with short larval competence periods: under laboratory conditions peak settlement typically occurs within 2-3 days of release (Harrison and Wallace, 1990). Thus the degree of connectivity between source and sink populations may be an important factor determining recovery in this species. It is likely that Agariciids are self-seeding on a reef scale, and if this is the case, they could become locally extinct in future due to their vulnerability to temperature change. These dynamics have been explored using hypothetical brooding and broadcasting coral species at different spatial scales and different levels of larval retention (Preece and Johnson, 1993); brooding corals only recovered from disturbances when the level of damage was low and connectivity between reefs high. In Belize, where *Agaricia tenuifolia* patch reefs were heavily impacted during the 1995 and 1998 warming events (>43% and >35% mortality respectively), recovery is predicted to be slow if at all (Aronson et al., 2000; Kramer and Kramer, 2000; McField, 1999).

Colpophyllia natans, like many Caribbean spawning species, has a low rate of recruitment, but was sufficiently fecund to nearly double in population size over the course of the first 50 years of the warming sequence. The size structure of the population appeared to stay constant during this period. Like the increases in *Agaricia* spp. this can be attributed to the sudden availability of space, and lack of competitors with the attrition of *M. annularis* and *S. michelinii* populations. However, at 60 years, *C. natans* began a rapid decline, which was concurrent with a shift towards smaller colony size classes. Unlike *Agaricia* spp., *C. natans* is less likely to rapidly face localised extinction, as they are broadcast spawners, (peak settlement under laboratory conditions occurs within 5-10 days of release (Harrison and Wallace, 1990), thus they can be considered one of the more resilient species in the assemblage.

Three species, *Meandrina meandrites*, *Eusmilia fastigiata* and *Madracis* spp., greatly increased both population and colony size during the sequence of warming events.

All of them are relatively rare species, occurring sporadically and forming small colonies. Three reasons may explain this:

1. It is possible that the parameter values for bleaching and thermally-induced mortality were underestimated, as these species have not often been included in bleaching reports (probably as a result of their naturally low abundance). If this is the case, it would be expected that their populations should be negatively affected by climate change, not enhanced.

2. Non-scleractinian groups not included in the model (apart from algae) but present in reef communities may occupy increasing amounts of newly created space, thus preventing expansion of *M. meandrina, E. fastigiata* and *Madracis* spp. This is supported by observations of sponge populations unimpacted or enhanced by warming in areas where corals declined (Vicente, 1990; Hughes, 1996).

3. An assumption that underpins the model is that colony growth is indeterminate (type II *sensu* Sebens, 1987), and colony size is a function of growth, competition and partial mortality. Size differences between coral species may suggest genetic constraints acting with the environment (Meesters et al., 2001). If this is the case, then it is likely that species increasing in abundance and colony size will be genetically constrained from doing so in reality.

However, the model behaviour may be realistic and these species may increase in abundance. This is supported by observations of *Madracis* species complex and its resistance to bleaching in the Dutch Antilles (Diekmann, pers comm.).

The model combined with HadCM3-derived climate predictions showed many characteristics of reef communities under stress from repeated warming events and other disturbances that have been observed in the field. It showed how changes to future climate could act at various scales, with impacts at population and community levels, and also how local factors such as reef connectivity and eutrophication may intensify the impact of warming events. This is the first model to date with this level of information.

Previous simulation studies have either applied size-classified matrix population models and examined the effects of various impacts on single species (Andres and Rodenhouse, 1993; Fong and Glynn, 2000; Hughes and Tanner, 2000) or used spatially explicit models of communities (usually hypothetical species) but with low spatial resolution so colony size structure information is absent, and analyses are based solely on less informative abundance data (Crimp and Braddock, 1993; Johnson and Preece, 1992; Karlson and Buss, 1984; Preece and Johnson, 1993; Reichelt et al., 1985). This appears to be the first model to include both high-resolution demographic information and community responses simultaneously, and is the first predictive attempt to quantify the impacts of climate change at a community level. Only two other authors have modelled aspects of climate change manifest as warming events on coral reefs. At a single species level, Fong and Glynn (2000) tackled this issue at a regional scale looking at population changes in *Gardinoseris planulata* and Muko et al. (2001b) employed a partial differential equation model to the dynamics of *Acropora hyacinthis* recovering from a bleaching event. At a community level, Muko et al. (2001a) investigated the relative importance of rates of recruitment, growth and mortality for a community composed of two coral morphotypes following a catastrophic disturbance (implied warming event). This was designed to look at recolonisation processes and the mechanisms that operate during recovery to structure the reef community and did not predict community responses to further warming events.

Application of the coral community model to climate change does, however, have its limitations, and although it has captured the essential behaviour of reef communities and dynamics of populations undergoing repeated impacts, ultimately it is a gross simplification of the system; only corals and algae are present. Real reef communities are composed of many more components interacting together and constitute one of the most ecologically complex and diverse systems on the planet. Also factors not included in these simulations can play a role in intensifying the impacts of warming events e.g. local stressors such as pollution, sedimentation, over-fishing or destructive fishing (Done, 1999) and secondary effects of warming such as increased disease prevalence (Hayes and Goreau, 1998; Kramer and Kramer, 2000; Ostrander et al., 2000). These factors are now seen to be operating ubiquitously across reefs of the Western Atlantic region; even the most isolated of reefs, such as

atolls off the coast of Belize bear signs of multiple stressors (Kramer and Kramer, 2000). As with any model, caution must be exercised when attempting to extrapolate model predictions to real reef scenarios.

If the model is accurate in its predictions with respect to coral community responses (although not necessarily timing, as discussed above), there will be enormous economic implications. Changes in community structure to more ephemeral species will affect reef accretion rates, especially the loss of the main reef-building species, *M. annularis*. This may alter the balance of reef growth vs. erosion, potentially leading to a net loss of reef structural material (calcium carbonate). Not only does the physical reef framework act as a barrier to wave energy and hence coastal erosion, but also its intrinsic topographic complexity provides habitat for a vast array of organisms, including commercially important fish and shellfish species. Algal reef does not usually have the same level of three-dimensionality required to support such diversity, thus coastal fisheries are likely to be affected too. These processes will be exacerbated by three other predicted implications of climate change not included in this model, namely aragonite saturation state (predicted to decrease with increased sea temperature, leading to a 14-30% decrease the calcification rates of corals by 2050, Kleypas et al., 1999), sea level rise (Done, 1999) and increased storm frequency and intensity (Pittock, 1999). Finally the value of reefs as tourist sites is likely to diminish. Tourism is the fastest growing economic sector associated with coral reefs and is set to double in the near future. The Caribbean region is heavily dependant on tourism, an estimated $90 billion dollars is generated annually by tourism in the Caribbean by over 1 hundred million tourist visitors (Jameson et al. 1995), and SCUBA diving alone is predicted to generate US$ 1 billion by the year 2005 (US Department of State, 1998). The economies of small island states dependant on this tourism are likely to be affected by the degradation of reefs through climate change. The ability to accurately predict its consequences is thus extremely important.

Chapter 8. Conclusions

8.1. The model

This coral community model can accurately simulate the dynamics of a coral community. A cellular automaton (CA) provided a good basis for several reasons:

1) Being spatially explicit, it allows the fundamental spatial aspect of reef communities to be simulated, and it accurately captured effects of limited space on major processes such as recruitment, growth and frequency of competitive interactions. This also allowed the distribution of disturbance across space to be explicitly explored.
2) The generation of population and community complexity from a 'bottom-up' approach was both intuitive and founded on known biology of the system. Processes driving complexity at higher levels are not always known, but by building complexity from a basic level using published attributes of coral species, reef community complexity is achieved, yeilding clear similarities to that of real reefs.
3) High spatial resolution of the model and its foundation at polyp level facilitated prediction of coral population size structure. This is a major advance over earlier CA approaches. Benefits from using this model include providing a powerful insight into how several key processes operate to structure coral populations. This also aided tracking of corals through time, through mechanisms such as fission, fusion and partial mortality, which have not been achieved from spatial models to date.
4) Mechanistic implementation of modules handling coral life history processes permitted effects of parameter changes to be analysed individually and their influence within the model tested.
5) Probabilistic iteration meant variability around key processes such as recruitment could be simulated (Chapter 4).

Comparison of size structures of species populations is the most rigorous test of this model's accuracy. It yielded a high degree of confidence in model predictions, as 1) coral colony size structures are extremely species-specific and 2) they are the result

of coral life history processes together with environmental effects (background disturbance). So, by accurately predicting coral population size structures, the model demonstrated its ability to simulate coral community dynamics.

Model accuracy was partly due to the way that background disturbance was implemented. The powerlaw model was highly successful at generating disturbed patches at realistic frequencies and intensities, as demonstrated in Chapter 3.

A restriction in the application of this model is the amount of parameters required to simulate a coral community. Rates for as many key processes as possible must be known. Estimates for several may be fairly broad, as for recruitment estimates, but some parameters showed considerable sensitivity, e.g. competitive rank and growth estimates. Because of this, this model would become increasing difficult to use on a highly diverse coral community. However, it proved highly successful for simulating a Caribbean coral community, which have been well described and have low species diversity compared with the Indian Ocean and Pacific biogeographic regions.

8.2. Major findings and implications

The first conclusion from the study on disturbance patch dynamics was the equal importance of patch size and area disturbed. This has profound implications for field workers measuring the amount of reef area cleared following impacts, as the distribution of this space as large or small patches is likely to have a strong influence on the rates of reef recovery e.g. following ship groundings. A second major finding was the relationship between the threshold of total and partial colony mortality and log-transformed modal colony size class. This relationship deviated slightly from that suggested by (Bak and Meesters, 1998), as here modal colony size classes had predominately partial mortality, i.e. the threshold did not fall at the modal size class but generally in the next size class down. Conclusions from this are that age and size in corals are decoupled at smaller sizes than previously predicted.

Sensitivity testing demonstrated model stability over a wide range of values. Changes to competitive rank had the most effect on the model. This was in agreement with previous models, though conclusions are difficult to draw, given the

unclear role of coral competition in structuring coral communities. Also demonstrated was the importance of interactive reach in mediating juvenile survival and the lack of influence of temporal variability in recruitment. Both these findings indicate post-settlement processes to be of greater importance than recruitment processes in structuring the coral community.

However the model does have limitations. Not all species originally included could be accurately predicted. Populations of *Siderastrea siderea* were consistently composed of smaller colonies than reported from real reefs. This was discussed in Chapter 5, and may be related to the life history of this species; the model may have highlighted an area where current information is lacking.

The observed response of the model to a single warming event highlights the varying consequences of such impacts depending on severity. Initial responses of coral communities closely mirrored those seen in past warming events, which suggests that the model is accurate in its predictions. However, lack of long-term monitoring data following real warming events in the Caribbean (the most significant event to date occurred in 1998) means that model accuracy over a decadal scale could not be fully assessed. Recovery times were variable, depending on algal growth and coral recruitment, demonstrating the importance of local setting on recovery rate. Algal cover has increased at many sites in the Caribbean in the past two decades (de Ruyter van Steveninck and Bak, 1986; Hughes, 1994; Liddell and Ohlhorst, 1987), indicating that the simulations with high algal growth rates may be the most realistic. Supply of coral recruits was also important in reef recovery. This has consequences both for areas with low connectivity where resident coral fecundity is decreased by warming and also for sites that have low recruitment through prior anthropogenic degradation (Richmond, 1993). Impacts of warming events in such areas are likely to have amplified consequences.

The application of repeated warming events forced the modelled coral community further and further away from its pre-disturbance state. Firstly, a shift in community structure occurred, as major reef-building coral species were replaced by more ephemeral ones, and secondly a phase shift occurred, where algae replaced corals. If predictions are correct, after 15 years (i.e. in 2015) reefs in Belize will have lost their

characteristic community structure, and will not return to such a state for at least a century. This result has enormous ecological consequences, as discussed in Chapter 7. However this result must also be viewed from within the framework of assumptions from which it was generated. Ongoing work into the ability of corals (Brown et al., 2002) and/or symbionts (Baker et al. 2002)[15] to acclimate or adapt to increasing sea temperature may show that coral adaptation can occur very quickly. Likewise, revised emissions scenarios and greatly reduced greenhouse effects, and advances in predictive power of global climate models may alter the sequence of warming events used here. This result, however, is based on current knowledge.

One of the most important conclusions regarding individual species is the vulnerability of *Montastraea annularis* to repeated warming events. The life history of this major reef building species means that population recovery is unlikely, and its current dominance on many Western Atlantic reefs may change in the near future. How this will affect the functioning of such reefs is uncertain, as this species complex is key to much of the framework, and hence indirectly to much of the high diversity of associated fauna.

8.3. Future directions

As more information on coral responses become available with every successive warming event, this model can be modified and assumptions revised. This work provides a thorough foundation for future research. Further efforts need not solely be restricted to warming events; many other types of disturbance could be applied, providing there is sufficient information on which to base assumptions.

One area of this model that could be further developed concerns algae. Previously disregarded as direct competitors with corals, ongoing work is showing that certainly corals do interact with macroalgae[16]. When more empirical work is published on the frequency and outcome of interactions with algae, this generic group could be split into macro-, turf and calcarious algae, with the former split further by species, with varying responses to competition with corals, nutrient enrichment and grazer

[15] ISRS European Meeting, September 2002.
[16] Nugues et al. preliminary findings presented at ISRS European meeting, September 2002.

removal. Supported by field experimentation, this model could be applied to questions regarding the dynamics of coral/algal dominance on reefs. The current work has already highlighted the complex influence of algae in mediating reef recovery, using the demonstrated but simplistic representation of algae; more specific representation will almost certainly generate interesting results.

This model could also be applied to meta-population studies, which could be carried out by linking several plots with varying degrees of connectivity (this has already been started for Great Barrier Reef communities, C. Johnson, pers. comm.). This could be used to predict the consequences of changes in patterns of larval dispersal on spatially separated populations, a highly topical area of study given the degradation of many Caribbean reefs in the last decades.

References

Adey, W. H., McConnaughey, T. A., Small, A. M. and Spoon, D. M. (2000). Coral reefs: endangered, biodiverse, genetic resources. In *Seas at the Millennium: An Environmental Evaluation*, (ed. C. Sheppard). Amsterdam: Elsevier Science Ltd.

Aerts, L. A. M. (1998). Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species identity and cover. *Marine Ecology Progress Series* **175**, 241-249.

Aerts, L. A. M. and van Soest, R. W. M. (1997). Quantification of sponge/coral interactions in a physically stressed reef community, NE Colombia. *Marine Ecology Progress Series* **148**, 125-134.

Andrefouet, S., Mumby, P. J., McField, M., Hu, C. and Muller-Karger, F. E. (2002). Revisiting coral reef connectivity. *Coral Reefs*.

Andres, N. G. and Rodenhouse, N. L. (1993). Resilience of corals to hurricanes - a simulation model. *Coral Reefs* **12**, 167-175.

Antonius, A. and Ballesteros, E. (1998). Epizoism: a new threat to coral health in Caribbean reefs. *Revista De Biologia Tropical* **46**, 145-156.

Aronson, R. B. and Precht, W. F. (2000). Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnology and Oceanography* **45**, 251-255.

Aronson, R. B. and Precht, W. F. (2001). White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* **460**, 25-38.

Aronson, R. B., Precht, W. F., Macintyre, I. G. and Murdoch, T. J. T. (2000). Coral bleach-out in Belize. *Nature* **405**, 36-36.

Babcock, R. C. (1984). Reproduction and Distribution of 2 Species of *Goniastrea* (Scleractinia) from the Great Barrier-Reef province. *Coral Reefs* **2**, 187-195.

Babcock, R. C. (1988). Fine scale spatial and temporal patterns in coral settlement. In *Proceedings of the 6th International Coral Reef Symposium*, Townsville, vol 2, pp. 635-639.

Babcock, R. C. (1991). Comparative demography of 3 species of scleractinian corals using age-dependent and size-dependent classifications. *Ecological Monographs* **61**, 225-244.

Baggitt, L. S. and Bright, T. J. (1985). Coral recruitment at the East Flower Garden reef (Northwestern Gulf of Mexico). In *Proceedings of the Fifth International Coral Reef Symposium, Tahiti*, Tahiti, vol 4, pp. 379-384.

Bak, R. P. M. (1983). Neoplasia, regeneration and growth in the reef-building coral *Acropora palmata*. *Marine Biology* **77**, 221-227.

Bak, R. P. M., Brouns, J. J. W. M. and Heys, F. M. L. (1977). Regeneration and aspects of spatial competition in the scleractinian corals. In *Proceedings of the 3rd International Coral Reef Symposium*, Miami, pp. 143148.

Bak, R. P. M. and Engel, M. S. (1979). Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Marine Biology* **54**, 341-352.

Bak, R. P. M. and Luckhurst, B. E. (1980). Constancy and change in coral reef habitats along depth gradients at Curacao. *Oecologia* **47**, 145-155.

Bak, R. P. M. and Meesters, E. H. (1997). Coral diversity, populations and ecosystem functioning. In *Proceedings of the 6th International Conference on Coelenterate Biology*, pp. 27-38.

Bak, R. P. M. and Meesters, E. H. (1998). Coral population structure: the hidden information of colony size-frequency distributions. *Marine Ecology Progress Series* **162**, 301-306.

Bak, R. P. M. and Meesters, E. H. (1999). Population structure as a response of coral communities to global change. *American Zoologist* **39**, 56-65.

Bak, R. P. M. and Nieuwland, G. (1995). Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. *Bulletin of Marine Science* **56**, 609-619.

Bak, R. P. M. and Steward van Es, Y. (1980). Regeneration of superficial damage in the Scleractinian Corals *Agaricia agaricites* F *purpurea* and *Porites astreoides*. *Bulletin of Marine Science* **30**, 883-887.

Bak, R. P. M., Termaat, R. M. and Dekker, R. (1982). Complexity of coral interactions - influence of time, location of interaction and epifauna. *Marine Biology* **69**, 215-222.

Baker, A. C. (2001). Reef corals bleach to survive change. *Nature* **411**, 765-766.

Barnes, D. J. and Chalker, B. E. (1990). Calcification and photosynthesis in reef-building corals and algae. In *Ecosystems of the World: Coral Reefs*, vol. 25 (ed. Z. Dubinsky), pp. 109-131.

Bender, E. A., Case, T. J. and Gilpin, M. E. (1984). Perturbation experiments in community ecology: theory and practice. *Ecology* **65**, 1-13.

Birkeland, C. (1977). The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. In *Proceedings of the 3rd International Coral Reef Symposium*, Miami, pp. 15-21.

Birkeland, C. (1997). Life and Death of Coral Reefs. New York: Chapman and Hall.

Black, K. P., Moran, P. J. and Hammond, L. S. (1991). Numerical models show coral reefs can be self-seeding. *Marine Ecology Progress Series* **74**, 1-11.

Bradbury, R. H. and Young, P. C. (1981). The race and the swift revisited, or is aggression between corals important? In *Proceedings of the 4th International Coral Reef Symposium*, Manila, vol 2, pp. 351-356.

Bray, R. J. and Curtis, J. T. (1957). An ordination of the upland forest communities of southern Winconsin. *Ecological Monographs* **27**, 325-349.

Brown, B. E. (1997). Adaptations of reef corals to physical environmental stress. *Advances in Marine Biology* **31**, 221-299.

Brown, B. E., Dunne, R. P., Goodson, M. S. and Douglas, A. E. (2002). Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs* **21**, 119-126.

Brown, B. E. and Suharsono. (1990). Damage and recovery of coral reefs affected by El Nino related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* **8**, 163-170.

Bryant, D., Burke, L., McManus, J. and Spalding, M. (1998). Reefs at risk: a map based indicator of threats to the world's coral reefs. Cambridge: World Resources Institute.

Buddemeier, R. W. and Fautin, D. G. (1993). Coral bleaching as an adaptive mechanism - a testable hypothesis. *Bioscience* **43**, 320-326.

Bunkley-Williams, L., Morelock, J. and Williams, E. H. (1991). Lingering effects of the 1987 mass bleaching of Puerto Rican coral reefs in mid to late 1988. *Journal of Aquatic Animal Health* **3**, 242-247.

Burrows, M. T. and Hawkins, S. J. (1998). Modelling patch dynamics on rocky shores using deterministic cellular automata. *Marine Ecology Progress Series* **167**, 1-13.

Bythell, J. C., Bythell, M. and Gladfelter, E. H. (1993a). Initial results of a long-term coral reef monitoring program: impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. *Journal of Experimental Marine Biology and Ecology* **172**, 171-183.

Bythell, J. C., Gladfelter, E. H. and Bythell, M. (1993b). Chronic and catastrophic natural mortality of 3 common Caribbean reef corals. *Coral Reefs* **12**, 143-152.

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P. and Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**, 477-500.

Carleton, J. H. and Sammarco, P. W. (1987). Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques. *Bulletin of Marine Science* **40**, 85-98.

Carlon, D. B. and Olson, R. R. (1993). Larval dispersal distance as an explanation for adult spatial pattern in 2 Caribbean reef corals. *Journal of Experimental Marine Biology and Ecology* **173**, 247-263.

Carricart-Ganivet, J. P., Beltran-Torres, A. U., Merino, M. and Ruiz-Zarate, M. A. (2000). Skeletal extension, density and calcification rate of the reef building coral *Montastraea annularis* (Ellis and Solander) in the Mexican Caribbean. *Bulletin of Marine Science* **66**, 215-224.

Chappell, J. (1980). Coral morphology, diversity and reef growth. *Nature* **286**, 249-252.

Chiappone, M. and Sullivan, K. M. (1996). Distribution, abundance and species composition of juvenile scleractinian corals in the Florida Reef Tract. *Bulletin of Marine Science* **58**, 555-569.

Chornesky, E. A. (1989). Repeated reversals during spatial competition between corals. *Ecology* **70**, 843-855.

Clarke, K. R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143.

Colgan, M. W. (1987). Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology* **68**, 1592-1605.

Connell, J. H. (1973). Population ecology of reef-building corals. In *Biology and Geology of Coral Reefs*, vol. 2 (ed. O. A. Jones and R. Endean). New York: Academic Press.

Connell, J. H. (1976). Competitive interactions and the species diversity of corals. In *Coelenterate Ecology and Behaviour*, (ed. G. O. Mackie), pp. 51-58. New York: Plenum Press.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302-1310.

Connell, J. H. (1985). The consequences of variation in initial settlement vs postsettlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93**, 11-45.

Connell, J. H. (1997). Disturbance and recovery of coral assemblages. *Coral Reefs* **16**, S101-S113.

Connell, J. H., Hughes, T. P. and Wallace, C. C. (1997). A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* **67**, 461-488.

Connell, J. H. and Keough, M. J. (1985). Disturbance and patch dynamics of subtidal marine animals on hard substrata. In *The Ecology of Natural Disturbance and Patch Dynamics*, (ed. S. T. A. Pickett and P. S. White), pp. 125-151. Orlando, Fl.: Academic Press.

Connell, J. H. and Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. *American Naturalist* **121**, 789-824.

Cope, M. (1981). Intespecific coral interactions in Hong Kong. In *Proceedings of the 4th International Coral Reef Symposium*, Manila, vol 2, pp. 357-362.

Courchamp, F., Clutton-Brock, T. and Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**, 405-410.

Coyer, J. A., Ambrose, R. F., Engle, J. M. and Carroll, J. C. (1993). Interactions between corals and algae on a temperate zone rocky reef: mediation by sea urchins. *Journal of Experimental Marine Biology and Ecology* **167**, 21-37.

Crimp, O. N. and Braddock, R. D. (1993). Simulation of coral reefs and crown of thorns starfish. *Environmetrics* **4**, 53-74.

De Nys, R., Coll, J. C. and Price, I. R. (1991). Chemically mediated interactions between the red alga *Plocamium hamatum* (Rhodophyta) and the octocoral *Sinularia cruciata* (Alcyonacea). *Marine Biology* **108**, 315-320.

de Ruyter van Steveninck, E. D. (1987). Ecological Studies of two abundant macroalgae on a Caribbean coral reef.

de Ruyter van Steveninck, E. D. and Bak, R. P. M. (1986). Changes in abundance of coral reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Marine Ecology Progress Series* **34**, 87-94.

de Ruyter van Steveninck, E. D., van Mulekom, L. L. and Breeman, A. M. (1988). Growth inhibition of *Lobophora variegata* (Lamouroux) Womersley by scleractinian corals. *Journal of Experimental Marine Biology and Ecology* **115**, 169-178.

Diaz-Pulido, G. and McCook, L. J. (2002). The fate of bleached corals: patterns and dynamics of algal recruitment. *Marine Ecology-Progress Series* **232**, 115-128.

Diekmann, O. E., Bak, R. P. M., Stam, W. T. and Olsen, J. L. (2001). Molecular genetic evidence for probable reticulate speciation in the coral genus *Madracis* from a Caribbean fringing reef slope. *Marine Biology* **139**, 221-233.

Dodge, R. E., Logan, A. and Antonius, A. (1982). Quantitative reef assessment studies in Bermuda - a comparison of methods and preliminary results. *Bulletin of Marine Science* **32**, 745-760.

Done, T. (1992). Constancy and change in some Great Barrier Reef coral communities - 1980-1990. *American Zoologist* **32**, 655-662.

Done, T. J. (1987). Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus *Porites*: evidence of population resilience. *Coral Reefs* **6**, 75-90.

Done, T. J. (1988). Simulation of recovery of pre-disturbance size structure in populations of *Porites* Spp. damaged by the crown of thorns starfish *Acanthaster planci*. *Marine Biology* **100**, 51-61.

Done, T. J. (1999). Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *American Zoologist* **39**, 66-79.

Dubinsky, Z. and Stambler, N. (1996). Marine pollution and coral reefs. *Global Change Biology* **2**, 511-526.

Dunstan, P. K. and Johnson, C. R. (1998). Spatio-temporal variation in cores recruitment at different scales on Heron Reef, southern Great Barrier Reef. *Coral Reefs* **17**, 71-81.

Dustan, P. and Halas, J. C. (1987). Changes in the reef coral community of Carysfort Reef, Key Largo, Florida - 1974 to 1982. *Coral Reefs* **6**, 91-106.

Edinger, E. N. and Browne, D. R. (2000). Continental Seas of Western Indonesia. In *Seas at the Millennium: an environmental evaluation*, vol. 2 (ed. C. Sheppard), pp. 381-404. Amsterdam, NL.: Elsevier Science Ltd.

Edmunds, P. J. (1994). Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching

susceptible clones. *Marine Biology* **121**, 137-142.

Edmunds, P. J. (2000). Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Marine Ecology-Progress Series* **202**, 113-124

Edmunds, P. J. and Carpenter, R. C. (2001). Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *PNAS*, 071524598.

Endean, R., Cameron, A. M. and DeVantier, L. M. (1988). *Acanthaster plancii* predation on massive corals: the myth of rapid recovery. Australia, vol 2, pp. 143-148.

Engel, S. and Pawlik, J. R. (2000). Allelopathic activities of sponge extracts. *Marine Ecology Progress Series* **207**, 273-281.

Fearon, R. J. and Cameron, A. M. (1997). Preliminary evidence supporting the ability of hermatypic corals to affect adversely larvae and early settlement stages of hard coral competitors. *Journal of Chemical Ecology* **23**, 1769-1780.

Fisk, D. A. and Done, T. (1985). Taxonomic and bathymetric patterns of bleaching in corals, Myrmidon reef (Queensland). In *Proceedings of the 5th International Coral Reef Congress*, Tahiti, vol 6, pp. 149-154.

Fitt, W. K., Brown, B. E., Warner, M. E. and Dunne, R. P. (2001). Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* **20**, 51-65.

Fitt, W. K., McFarland, F. K., Warner, M. E. and Chilcoat, G. C. (2000). Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnology and Oceanography* **45**, 677-685.

Fitt, W. K., Spero, H. J., Halas, J., White, M. W. and Porter, J. W. (1993). Recovery of the coral *Montastraea annularis* in the Florida Keys after the 1987 Caribbean bleaching event. *Coral Reefs* **12**, 57-64.

Fitt, W. K. and Warner, M. E. (1995). Bleaching patterns of four species of Caribbean reef corals. *Biological Bulletin* **189**, 298-307.

Fong, P. and Glynn, P. W. (1998). A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the Eastern Pacific? *Marine Biology* **130**, 663-674.

Fong, P. and Glynn, P. W. (2000). A regional model to predict coral population dynamics in response to El Nino-Southern Oscillation. *Ecological Applications* **10**, 842-854.

Fricke, H. and Meischner, D. (1985). Depth limits of Bermudan scleractinian corals - a submersible survey. *Marine Biology* **88**, 175-187.

Gaines, S. and Roughgarden, J. (1985). Larval settlement rate - a leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences of the United States of America* **82**, 3707-3711.

Gates, R. D. and Edmunds, P. J. (1999). The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* **39**, 30-43.

Gattuso, J. P., Allemand, D. and Frankignoulle, M. (1999). Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. *American Zoologist* **39**, 160-183.

Geister, J. (1977). The influence of wave exposure on the ecological zonation of Caribbean coral reefs. In *3rd International Coral Reef Symposium*, Miami, pp. 23-29.

Ghiold, J. and Smith, S. H. (1990). Bleaching and recovery of deep water, reef-dwelling invertebrates in the Cayman Islands, B.W.I. *Caribbean Journal of Science* **26**, 52-61.

Gladfelter, E. H., Monohan, R. K. and Gladfelter, W. B. (1978). Growth rates of five reef-building corals in the northeastern Caribbean. *Bulletin of Marine Science* **28**, 728-734.

Gleason, M. G. (1996). Coral recruitment in Moorea, French Polynesia: The importance of patch type and temporal variation. *Journal of Experimental Marine Biology and Ecology* **207**, 79-101.

Gleeson, M. W. and Strong, A. E. (1995). Applying MCSST to coral reef bleaching. In *Satellite Monitoring of the Earth's Surface and Atmosphere*, vol. 16, pp. 151-154.

Glynn, P. W. (1988). El Nino Southern Oscillation 1982-1983: nearshore population, community, and ecosystem responses. *Annual Review of Ecology and Systematics* **19**, U309-&.

Glynn, P. W. (1993). Coral reef bleaching - ecological perspectives. *Coral Reefs* **12**, 1-17.

Glynn, P. W. (1996). Coral reef bleaching: Facts, hypotheses and implications. *Global Change Biology* **2**, 495-509.

Goreau, T. F. (1959). The Ecology of Jamaican Coral Reefs. 1. Species Composition and Zonation. In *The Ecology of Jamaican Coral Reefs*, pp. 67-90.

Goreau, T. J. (1992). Bleaching and reef community change in Jamaica - 1951-1991. *American Zoologist* **32**, 683-695.

Goreau, T. J. and Macfarlane, A. H. (1990). Reduced growth rate of *Montastraea annularis* following the 1987-1988 coral bleaching event. *Coral Reefs* **8**, 211-215.

Goreau, T. J., McClanahan, T. R., Hayes, R. L. and Strong, A. E. (2000). Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* **14**, 5-15.

Gosselin, L. A. and Qian, P. Y. (1997). Juvenile mortality in benthic marine invertebrates. *Marine Ecology-Progress Series* **146**, 265-282.

Grassle, J. F. (1973). Variety in coral reef communities. In *Biology and Geology of Coral Reefs*, vol. 2 (ed. O. A. Jones and R. Endean), pp. 247-270. New York: Academic Press.

Graus, R. R. and Macintyre, I. G. (1989). The zonation patterns of Caribbean coral reefs as controlled by wave and light energy input, bathymetric setting and reef morphology: computer-simulation experiments. *Coral Reefs* **8**, 9-18.

Graus, R. R., Macintyre, I. G. and Herchenroder, B. E. (1984). Computer-simulation of the reef zonation at Discovery Bay, Jamaica - hurricane disruption and long-term physical oceanographic controls. *Coral Reefs* **3**, 59-68.

Gunderson, L. H. (2000). Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics* **31**, 425-439.

Guzman, H. M., Burns, K. A. and Jackson, J. B. C. (1994). Injury, regeneration and growth of Caribbean reef corals after a major oil spill in Panama. *Marine Ecology Progress Series* **105**, 231-241.

Guzman, H. M. and Holst, I. (1993). Effects of chronic oil-sediment pollution on the reproduction of the Caribbean reef coral *Siderastrea siderea*. *Marine Pollution Bulletin* **26**, 276-282.

Guzman, H. M., Jackson, J. B. C. and Weil, E. (1991). Short-term ecological consequences of a major oil spill on Panamanian subtidal reef corals. *Coral Reefs* **10**, 1-12.

Hall, V. R. and Hughes, T. P. (1996). Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* **77**, 950-963.

Harriott, V. J. (1985). Mortality rates of scleractinian corals before and during a mass bleaching event. *Marine Ecology Progress Series* **21**, 81-88.

Harriott, V. J. and Fisk, D. A. (1987). A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Marine Ecology Progress Series* **37**, 201-208.

Harrison, P. L., Babcock, R. C., Bull, G. D., Oliver, J. K., Wallace, C. C. and Willis, B. L. (1984). Mass spawning in tropical reef corals. *Science* **223**, 1186-1189.

Harrison, P. L. and Wallace, C. C. (1990). Reproduction, dispersal and recruitment of scleractinian corals. In *Ecosystems of the World: Coral Reefs*, vol. 2 (ed. Z. Dubinsky), pp. 133-207.

Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofmann, E. E., Lipp, E. K., Osterhaus, A., Overstreet, R. M. et al. (1999). Emerging marine diseases: climate links and anthropogenic factors. *Science* **285**, 1505-1510.

Hayes, R. L. and Goreau, N. I. (1998). The significance of emerging diseases in the tropical coral reef ecosystem. *Revista De Biologia Tropical* **46**, 173-185.

Heyward, A. J. and Negri, A. P. (1999). Natural inducers of coral larval metamorphosis. *Coral Reefs* **18**, 273-279.

Hidaka, M. (1985). Nematocyst discharge, histoincompatibility, and the formation of sweeper tentacles in the coral *Galaxea fascicularis*. *Biological Bulletin* **168**, 350-358.

Highsmith, R. C. (1982). Reproduction by fragmentation in corals. *Marine Ecology Progress Series* **7**, 207-226.

Highsmith, R. C., Lueptow, R. L. and Schonberg, S. C. (1983). Growth and bioerosion of 3 massive corals on the Belize barrier reef. *Marine Ecology Progress Series* **13**, 261-271.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**, 839-866.

Hoegh-Guldberg, O. and Smith, G. J. (1989). The effect of sudden changes in temperature, irradiance and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* (Esper 1797) and *Seriatopora hystrix* (Dana 1846). *Journal of Experimental Marine Biology and Ecology* **129**, 279-303.

Hughes, T. P. (1984). Population dynamics based on individual size rather than age: a general model with a reef coral example. *American Naturalist* **123**, 778-795.

Hughes, T. P. (1985). Life histories and population dynamics of early successional corals. In *Proceedings of the Fifth International Coral Reef Symposium*, Tahiti, vol 4, pp. 101-106.

Hughes, T. P. (1989). Community structure and diversity of coral reefs: the role of history. *Ecology* **70**, 275-279.

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547-1551.

Hughes, T. P. (1996). Demographic approaches to community dynamics: A coral reef example. *Ecology* 77, 2256-2260.

Hughes, T. P., Ayre, D. and Connell, J. H. (1992). The evolutionary ecology of corals. *Trends in Ecology & Evolution* 7, 292-295.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E. and Willis, B. L. (1999). Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* **397**, 59-63.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E. and Willis, B. L. (2000). Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* **81**, 2241-2249.

Hughes, T. P. and Connell, J. H. (1999). Multiple stressors on coral reefs: a long-term perspective *Limnology and Oceanography* **44**, 932-940.

Hughes, T. P. and Jackson, J. B. C. (1980). Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. *Science* **209**, 713-719.

Hughes, T. P. and Jackson, J. B. C. (1985). Population dynamics and life histories of foliaceous corals. *Ecological Monographs* **55**, 141-166.

Hughes, T. P. and Tanner, J. E. (2000). Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* **81**, 2250-2263.

Humann, P. (2001). Reef Coral Identification. Florida: New World Publicatons Inc.

Huston, M. (1985). Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs* **4**, 19-25.

Inghe, O. (1989). Genet and ramet survivorship under different mortality regimes: a cellular automata model. *Journal of Theoretical Biology* **138**, 257-270.

IPCC. (1992). Climate Change 1992: The Supplimentary Report to the IPCC Scientific Assessment. Cambridge: Intergovernmentary Panel on Climate Change.

IPCC. (1996). Climate Change 1995: The Science of Climate Change. Contribution of Working Group 1 to the Second Assessment Report of IPCC. Cambridge: Intergovernmenary Panel on Climate Change.

IPCC. (2001). CLIMATE CHANGE 2001: THE SCIENTIFIC BASIS. Cambridge: Intergovernmentary Panel on Climate Change.

Johnson, C. R. and Preece, A. L. (1992). Damage, scale and recovery in model coral communities: the importance of system state. In *Proceedings of the 7th International Coral Reef Symposium*, Guam, vol 1, pp. 606-615.

Jokiel, P. L. and Coles, S. L. (1977). Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology* **43**, 201-208.

Jokiel, P. L. and Coles, S. L. (1990). Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* **8**, 155-162.

Jompa, J. and McCook, L. J. (1998). Seaweeds save the reefs?! Sargassum canopy decreases coral bleaching on inshore reefs. *Reef Resources* **8**, 5.

Jompa, J. and McCook, L. J. (2002). Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology* **271**, 25-39.

Karlson, R. H. (1980). Alternative competitive strategies in a periodically disturbed habitat. *Bulletin of Marine Science* **30**, 894-900.

Karlson, R. H. (1999). Dynamics of coral communities. Dordrecht, Boston, London: Kluwer.

Karlson, R. H. and Buss, L. W. (1984). Competition, disturbance and local diversity patterns of substratum-bound conal organisms: a simulation. *Ecological Modelling* **23**, 243-255.

Karlson, R. H. and Cornell, H. V. (1998). Scale-dependent variation in local vs. regional effects on coral species richness. *Ecological Monographs* **68**, 259-274.

Karlson, R. H. and Hurd, L. E. (1993). Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs* **12**, 117-125.

Karlson, R. H. and Jackson, J. B. C. (1981). Competitive networks and community structure: a simulation study. *Ecology* **62**, 670-678.

Kinzie, R. A., Takayama, M., Santos, S. R. and Coffroth, M. A. (2001). The adaptive bleaching hypothesis: experimental tests of critical assumptions. *Biological Bulletin* **200**, 51-58.

Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J. P., Langdon, C. and Opdyke, B. N. (1999). Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**, 118-120.

Knowlton, N. (1992). Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* **32**, 674-682.

Knowlton, N (2001). The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 5419-5425.

Kramer, P. A. and Kramer, P. R. (2000). Ecological status of the MesoAmerican Barrier Reef System. Miami: RSMAS.

Lang, J. C. (1971). Interspecific aggression by scleractinian corals. 1. The rediscovery of *Scolymia cubensis* (Milne Edwards & Haime). *Bulletin of Marine Science* **21**, 952-959.

Lang, J. C. (1973). Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bulletin of Marine Science* **23**, 260-279.

Lang, J. C. and Chornesky, E. A. (1990). Competition between scleractinian reef corals: a review of mechanisms and effects. In *Coral Reefs*, (ed. Z. Dubinsky), pp. 209-251. Amsterdam: Elsevier Science Publishers.

Lang, J. C., Lasker, H. R., Gladfelter, E. H., Hallock, P., Jaap, W. C., Losada, F. J. and Muller, R. G. (1992). Spatial and temporal variability during periods of recovery after mass bleaching on Western Atlantic coral reefs. *American Zoologist* **32**, 696-706.

Lang, J. C., Wicklund, R. I. and Dill, R. F. (1988). Depth- and habitat-related bleaching of zooxanthellate reef organisms near Lee Stocking Island, Exuma Cays, Bahamas. In *Proceedings of the 6th International Coral Reef Symposium*, Townsville, Australia, vol 3, pp. 269-274.

Langmead, O. and Chadwick-Furman, N. E. (1999). Marginal tentacles of the corallimorpharian *Rhodactis rhodostoma*. 1. Role in competition for space. *Marine Biology* **134**, 479-489.

Lasker, H. R. and Coffroth, M. A. (1999). Responses of clonal reef taxa to environmental change. *American Zoologist* **39**, 92-103.

Lasker, H. R., Peters, E. C. and Coffroth, M. A. (1984). Bleaching of reef coelenterates in the San Blas Islands, Panama. *Coral Reefs* **3**, 183-190.

Leder, J. J., Szmant, A. M. and Swart, P. K. (1991). The effect of prolonged bleaching on skeletal banding and stable isotopic composition in *Montastrea annularis*: preliminary observations. *Coral Reefs* **10**, 19-27.

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology* **73**, 1943-1967.

Lewin, R. (1986). Supply-side ecology. *Science* **234**, 25-27.

Lewis, J. B. (1970). Spatial distribution and pattern of some Atlantic reef corals. *Nature* **227**, 1158-1159.

Lewis, J. B. (1997). Abundance, distribution and partial mortality of the massive coral *Siderastrea siderea* on degrading coral reefs at Barbados, West Indies. *Marine Pollution Bulletin* **34**, 622-627.

Licuanan, W. Y. and Bakus, G. J. (1992). Coral spatial distributions: The ghost of competition past roused? In *Proceedings of the 7th International Coral Reef Symposium*, Guam, vol 1, pp. 545-549.

Liddell, W. D. (1992). Ten years of disturbance and change on a Jamaican fringing reef. In *Proceedings of the 7th International Coral Reef Symposium*, Guam, vol 1, pp. 144-155.

Liddell, W. D. and Ohlhorst, S. L. (1987). Patterns of reef community structure, North Jamaica. *Bulletin of Marine Science* **40**, 311-329.

Lirman, D. (2001). Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* **19**, 392-399.

Logan, A. (1984). Interspecific aggression in hermatypic corals from Bermuda. *Coral Reefs* **3**, 131-138.

Lough, J. M. and Barnes, D. J. (2000). Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* **245**, 225-243.

Loya, Y. (1976a). Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bulletin of Marine Science* **26**, 450-466.

Loya, Y. (1976b). Recolonisation of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* **57**, 278-289.

Maguire, L. A. and Porter, J. W. (1977). A spatial model of growth and competition strategies in coral communities. *Ecological Modelling* **3**, 249-277.

Mascarelli, P. E. and Bunkley-Williams, L. (1999). An experimental field evaluation of healing in damaged, unbleached and artificially bleached star coral, *Montastraea annularis*. *Bulletin of Marine Science* **65**, 577-586.

McClanahan, T. R., McField, M., Huitric, M., Bergman, K., Sala, E., Nystrom, M., Nordemar, I., Elfwing, T. and Muthiga, N. A. (2001a). Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs* **19**, 367-379.

McClanahan, T. R., Muthiga, N. A. and Mangi, S. (2001b). Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* **19**, 380-391.

McClanahan, T. R., Sheppard, C. R. C. and Obura, D. O. (2000). Coral Reefs of the Indian Ocean. Their Ecology and Conservation. New York: Oxford University Press, Inc.

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* **18**, 357-367.

McCook, L. J. (2001). Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. *Coral Reefs* **19**, 419-425.

McCook, L. J., Jompa, J. and Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* **19**, 400-417.

McField, M. D. (1999). Coral response during and after mass bleaching in Belize. *Bulletin of Marine Science* **64**, 155-172.

McGrath, T. A. and Smith, G. W. (1998). The effects of the 1995/1996 Western Atlantic coral bleaching event on the patch reefs around San Salvador Island, Bahamas. *Revista De Biologia Tropical* **46**, 91-99.

Meesters, E. H. and Bak, R. P. M. (1993). Effects of coral bleaching on tissue regeneration potential and colony survival. *Marine Ecology Progress Series* **96**, 189-198.

Meesters, E. H., Hilterman, M., Kardinaal, E., Keetman, M., de Vries, M. and Bak, R. P. M. (2001). Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Marine Ecology Progress Series* **209**, 43-54.

Meesters, E. H., Noordeloos, M. and Bak, R. P. M. (1994). Damage and regeneration: links to growth in the reef-building coral *Montastrea annularis*. *Marine Ecology Progress Series* **112**, 119-128.

Meesters, E. H., Wesseling, I. and Bak, R. P. M. (1997). Coral colony tissue damage in six species of reef-building corals: Partial mortality in relation with depth and surface area. *Journal of Sea Research* **37**, 131-144.

Miller, M. W. (1988). Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanography and Marine Biology: An Annual Review* **36**, 65-96.

Miller, M. W. and Hay, M. E. (1996). Coral-seaweed-grazer-nutrient interactions on temperate reefs. *Ecological Monographs* **66**, 323-344.

Miller, M. W., Weil, E. and Szmant, A. M. (2000). Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* **19**, 115-123.

Muko, S., Sakai, K. and Iwasa, Y. (2001a). Dynamics of marine sessile organisms with space-limited growth and recruitment: Application to corals. *Journal of Theoretical Biology* **210**, 67-80.

Muko, S., Sakai, K. and Iwasa, Y. (2001b). Size distribution dynamics for a marine sessile organism with space-limitation in growth and recruitment: application to a coral population. *Journal of Animal Ecology* **70**, 579-589.

Mumby, P. J. (1999). Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Marine Ecology-Progress Series* **190**, 27-35.

Munro, J. L. (1996). The scope of tropical reef fisheries and their management. In *Reef Fisheries*, (ed. N. V. C. Polunin and C. M. Roberts), pp. 1-14. London: Chapman and Hall.

Nagelkerken, I., Meesters, E. H. and Bak, R. P. M. (1999). Depth-related variation in regeneration of artificial lesions in the Caribbean corals *Porites astreoides* and *Stephanocoenia michelinii*. *Journal of Experimental Marine Biology and Ecology* **234**, 29-39.

Neudecker, S. (1979). Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology* **60**, 666-672.

Oakley, S. G. and Pilcher, N. (2000). Blastfishing. In *Seas at the Millennium: an environmental evaluation*, vol. 2 (ed. C. Sheppard). Amsterdam, NL.: Elsevier Science Ltd.

Omori, M., Fukami, H., Kobinata, H. and Hatta, M. (2001). Significant drop of fertilization of *Acropora* corals in 1999. An after-effect of heavy coral bleaching? *Limnology and Oceanography* **46**, 704-706.

Ostrander, G. K., Armstrong, K. M., Knobbe, E. T., Gerace, D. and Scully, E. P. (2000). Rapid transition in the structure of a coral reef community: The effects of coral bleaching and physical disturbance. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 5297-5302.

Pearson, R. G. (1981). Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* **4**, 105-122.

Pittock, A. B. (1999). Coral reefs and environmental change: Adaptation to what? *American Zoologist* **39**, 10-29.

Pomerance, R. (1999). Coral bleaching, coral mortality and global climate change. Report presented by Deputy Assistant Secretary of State for the Environment and Development to the US Coral Reef Task Force, 5 March 1999, Maui, Hawaii.

Porter, J. W., Lewis, S. K. and Porter, K. G. (1999). The effect of multiple stressors on the Florida Keys coral reef ecosystem: A landscape hypothesis and a physiological test. *Limnology and Oceanography* **44**, 941-949.

Porter, J. W. and Meier, O. W. (1992). Quantification of loss and change in Floridian reef coral populations. *American Zoologist* **32**, 625-640.

Potts, D. C. (1977). Suppression of coral populations by filamentous algae within damselfish territories. *Journal of Experimental Marine Biology and Ecology* **28**, 207-216.

Preece, A. L. and Johnson, C. R. (1993). Recovery of model coral communities: complex behaviours from interaction of parameters operating at different spatial scales. In *Complex Systems: from Biology to Computation*, (ed. D. G. Green and T. Bossomaier), pp. 69-81. Amsterdam: IOS Press.

Quinn, N. J. and Kojis, B. L. (1999). Subsurface seawater temperature variation and the recovery of corals from the 1993 coral bleaching event in waters off St. Thomas, US Virgin Islands. *Bulletin of Marine Science* **65**, 201-214.

Raimondi, P. T. and Morse, A. N. C. (2000). The consequences of complex larval behavior in a coral. *Ecology* **81**, 3193-3211.

Reaka-Kudla, M. L. (1997). In *Biodiversity II: Understanding and Protecting our Biological Resources*, (ed. M. L. Reaka-Kudla, Wilson, D. E. & Wilson, E. O.), pp. 83-108. Washington DC: Joseph Henry Press.

Reichelt, R. E., Green, D. G. and Bradbury, R. H. (1985). Discrete simulation of cyclone effects on the spatial patterns and community structure of a coral reef. In *Proceedings of the Fifth International Coral Reef Symposium, Tahiti*, Tahiti, vol 3, pp. 337-341.

Reichelt, R. E., Loya, Y. and Bradbury, R. H. (1986). Patterns in the use of space by benthic communities on 2 coral reefs of the Great Barrier Reef. *Coral Reefs* **5**, 73-79.

Rice, S. A. and Hunter, C. L. (1992). Effects of suspended sediment and burial on scleractinian corals from West Central Florida patch reefs. *Bulletin of Marine Science* **51**, 429-442.

Richmond, R. H. (1993). Coral reefs - Present problems and future concerns resulting from anthropogenic disturbance. *American Zoologist* **33**, 524-536.

Rinkevich, B. and Loya, Y. (1985). Intraspecific competition in a reef coral: effects on growth and reproduction. *Oecologia* **66**, 100-105.

Roberts, C. M. (1993). Coral reefs - Health, hazards and history. *Trends in Ecology & Evolution* **8**, 425-427.

Roberts, C. M. (1997). Connectivity and management of Caribbean coral reefs. *Science* **278**, 1454-1457.

Rogers, C. S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**, 185-202.

Rogers, C. S. (1993). Hurricanes and coral reefs - the intermediate disturbance hypothesis revisited. *Coral Reefs* **12**, 127-137.

Rogers, C. S., Fitz, H. C., Gilnack, M., Beets, J. and Hardin, J. (1984). Scleractinian coral recruitment patterns at Salt River submarine canyon, St Croix, United States Virgin Island. *Coral Reefs* **3**, 69-76.

Romano, S. L. (1990). Long-term effects of interspecific aggression on growth of the reef-building corals *Cyphastrea ocellina* (Dana) and *Pocillopora damicornis* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **140**, 135-146.

Rosen, B. R. and Taylor, J. D. (1969). Reef coral from Aldabra: new mode of reproduction. *Science* **166**, 119-121.

Ross, M. A. and Harper, J. L. (1972). Occupation of biological space during seedling establishment. *Ecology* **58**, 467-485.

Roughgarden, J., Iwasa, Y. and Baxter, C. (1985). Demographic theory for an open marine population with space-limited recruitment. *Ecology* **66**, 54-67.

Rowan, R. and Knowlton, N. (1995). Intraspecific diversity and ecological zonation in coral-algal symbiosis. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 2850-2853.

Rylaarsdam, K. W. (1983). Life histories and abundance patterns of colonial corals on Jamaican reefs. *Marine Ecology Progress Series* **13**, 249-260.

Sammarco, P. W. (1980). *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *Journal of Experimental Marine Biology and Ecology* **45**, 245-272.

Sammarco, P. W. (1982). Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *Journal of Experimental Marine Biology and Ecology* **61**, 31-55.

Sammarco, P. W. (1985). The Great Barrier Reef vs. the Caribbean: comparisons of grazers, coral recruitment patterns and reef recovery. In *Proceedings of the 5th International Coral Reef Symposium*, Tahiti, vol 4, pp. 391-397.

Sammarco, P. W. (1991). Geographically specific recruitment and post-settlement mortality as influences on coral communities: the cross-continental shelf transplant experiment. *Limnology and Oceanography* **36**, 496-514.

Sebens, K. P. (1976). The ecology of Caribbean sea anemones in Panama: utilization of space on a coral reef. In *Coelenterate Biology and Behaviour*, (ed. G. O. Mackie), pp. 67-77. New York: Plenum Press.

Sebens, K. P. (1987). The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics* **18**, 371-407.

Sebens, K. P. (1994). Biodiversity of coral reefs - what are we losing and why? *American Zoologist* **34**, 115-133.

Shannon, C. E. and Weaver, W. (1948). The mathematical theory of communication. Urbana, Illinois: University of Ilinois Press.

Sheppard, C. (2002). The main issues affecting coasts of the Indian and Western Pacific Ocean : a meta-analysis from *Seas at the Millennium. Marine Pollution Bulletin* **42**, 1179-1207.

Sheppard, C. and Rayner, N. A. (2002). Utility of the Hadley Centre sea ice and sea surface temperature data set (HadISST1) in two widely contrasting reef areas. *Marine Pollution Bulletin* **44**, 303-308.

Sheppard, C. R. C. (1979). Interspecific aggression between reef corals with reference to their distribution. *Marine Ecology Progress Series* **1**, 237-247.

Sheppard, C. R. C. (1981). The reef and soft-substrate coral fauna of Chagos, Indian Ocean. *Journal of Natural History* **15**, 607-621.

Sheppard, C. R. C. (1982). Coral populations on reef slopes and their major controls. *Marine Ecology Progress Series* **7**, 83-115.

Sheppard, C. R. C. (1985a). 'Reach' of aggressively interacting corals, and relative importance of interactions at different depths. In *Proceedings of the 4th International Coral Reef Symposium*, Manila, vol 2, pp. 263-368.

Sheppard, C. R. C. (1985b). Unoccupied substrate in the central Great Barrier Reef: role of coral interactions. *Marine Ecology Progress Series* **25**, 259-268.

Sheppard, C. R. C. (1999). Coral decline and weather patterns over 20 years in the Chagos Archipelago, central Indian Ocean. *Ambio* **28**, 472-478.

Sheppard, C. R. C., Spalding, M., Bradshaw, C. and Wilson, S. (2002). Erosion vs. recovery of coral reefs after 1998 el Nino: Chagos Reefs, Indian Ocean. *Ambio* **31**, 40-48.

Shulman, M. J. and Robertson, D. R. (1996). Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990. *Coral Reefs* **15**, 231-236.

Smith, S. R. (1992). Patterns of coral recruitment and postsettlement mortality on Bermuda's reefs: comparisons to Caribbean and Pacific reefs. *American Zoologist* **32**, 663-673.

Smith, S. V. and Buddemeier, R. W. (1992). Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics* **23**, 89-118.

Sokal, R. R. and Rohlf, F. J. (1995). Biometry: The principles and practice of statistics in biological research. New York: W. H. Freeman and Co.

Soong, K. (1993). Colony size as a species character in massive reef corals. *Coral Reefs* **12**, 77-83.

Suzuki, A., Kawahata, H., Tanimoto, Y., Tsukamoto, H., Gupta, L. P. and Yukino, I. (2000). Skeletal isotopic record of a *Porites* coral during the 1998 mass bleaching event *Geochemical Journal* **34**, 321-329.

Szmant, A. M. (1986). Reproductive ecology of Caribbean reef corals. *Coral Reefs* **5**, 43-53.

Szmant, A. M. and Gassman, N. J. (1990). The effects of prolonged bleaching on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* **8**, 217-224.

Szmant-Froelich, A. M. (1985a). The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). In *Proceedings of the 5th International Coral Reef Symposium.*, Tahiti, vol 4, pp. 295-300.

Szmant-Froelich, A. M. (1985b). Reproduction and recruitment of corals: conclusion. In *Proceedings of the 5th International Coral Reef Symposium*, Tahiti, vol 4, pp. 399-400.

Tanner, J. E. (1992). Experimental analysis of digestive hierarchies in coral assemblages. In *Proceedings of the 7th International Coral Reef Symposium*, Guam, vol 1, pp. 569-574.

Tanner, J. E. (1995). Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology* **190**, 151-168.

Tanner, J. E. (1997). Interspecific competition reduces fitness in scleractinian corals. *Journal of Experimental Marine Biology and Ecology* **214**, 19-34.

Tanner, J. E., Hughes, T. P. and Connell, J. H. (1994). Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology* **75**, 2204-2219.

Tomascik, T. (1991). Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West-Indies. *Marine Ecology Progress Series* **77**, 261-269.

Tunnicliffe, V. (1979). The role of boring sponges in coral fracture. In *Biologie des Spongiaires*, vol. 291 (ed. C. Levi and N. Boury-Esnault), pp. 309-315. Paris.

Turner, J., Hardman, E., Klaus, R., Fagoonee, I., Daby, D., Baghooli, R. and Persands, S. (2000). The reefs of Mauritius. In *Coral Reef Degradation in the Indian Ocean*, vol. 3 (ed. D. Souter D. Obura and O. Linden). Stockholm: CORDIO/SAREC.

Turner, S. J. (1994). The biology and population outbreaks of the corallivorous gastropod *Drupella* on Indo-Pacific reefs. *Oceanography and Marine Biology* **32**, 461-530.

van Moorsel, G. W. N. M. (1983). Reproductive strategies in 2 closely related stony corals (*Agaricia*, Scleractinia). *Marine Ecology Progress Series* **13**, 273-283.

van Moorsel, G. W. N. M. (1985). Disturbance and growth of juvenile corals (*Agaricia humilis* and *Agaricia agaricites*, scleractinia) in natural habitats on the reef of Curacao. *Marine Ecology Progress Series* **24**, 99-112.

van Moorsel, G. W. N. M. (1989). Juvenile ecology and reproductive strategies. Rijksuniversitatt Groningen, Netherlands.

Veron, J. E. N. (1986). Corals of Australia and the Indo-Pacific.: Hawaii University Press.

Veron, J. E. N. (2000). Corals of the World. Townsville: Australian Institute of Marine Science.

Vicente, V. P. (1990). Response of sponges with autotrophic endosymbionts during the coral bleaching episode in Puerto Rico. *Coral Reefs* **8**, 199-202.

Wallace, C. C. (1985). Reproduction, recruitment and fragmentation in 9 sympatric species of the coral genus *Acropora*. *Marine Biology* **88**, 217-233.

Weil, E. and Knowlton, N. (1994). A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its 2 sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895). *Bulletin of Marine Science* **55**, 151-175.

Wellington, G. M. (1982). Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecological Monographs* **52**, 223-241.

Wilkinson, C. (2000). Status of Coral Reefs of the World: 2000. Townsville: Australian Institute of Marine Science.

Wilkinson, C. and Hodgson, G. (1999). Coral reefs and the 1997-1998 mass bleaching and mortality. *Nature & Resources* **35**, 16-25.

Wilkinson, C. R. (1999). Global and local threats to coral reef functioning and existence: review and predictions. *Marine and Freshwater Research* **50**, 867-878.

Williams, E. H. and Bunkley-Williams, L. (1988). Bleaching of Caribbean coral reef symbionts in 1987-1988. In *Proceedings of the 6th International Coral Reef Symposium*, Townsville, vol 3, pp. 313-318.

Witman, J. D. (1992). Physical disturbance and community structure of exposed and protected reefs: a case study from St John, United States Virgin Islands. *American Zoologist* **32**, 641-654.

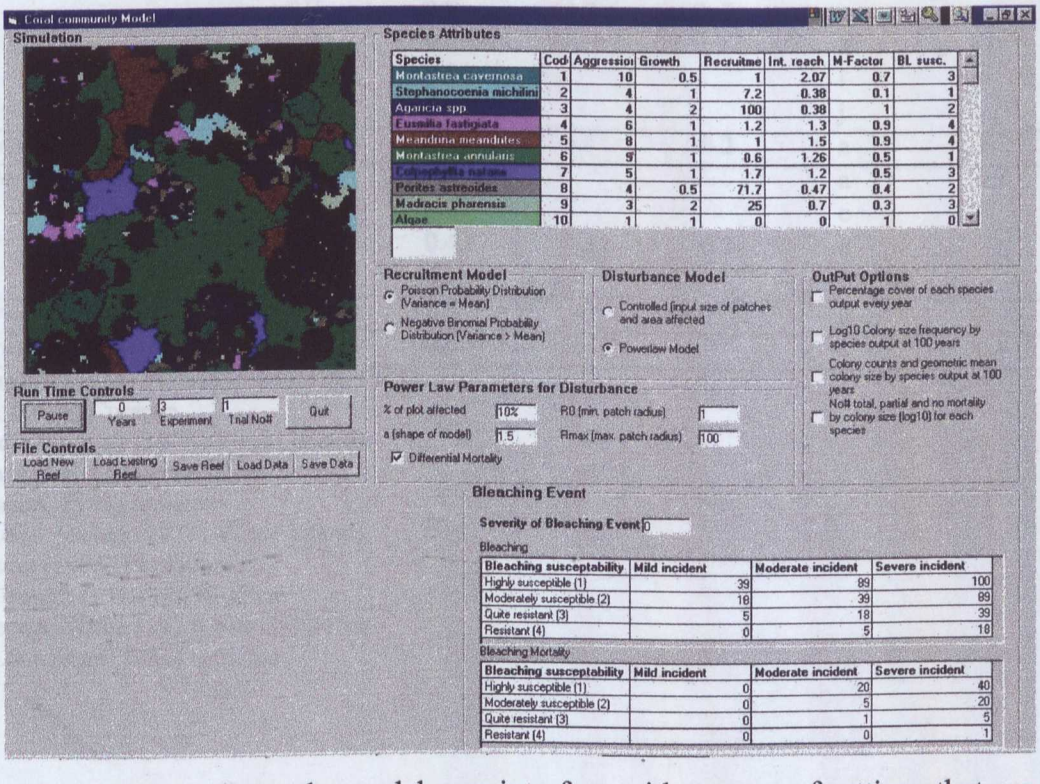
Woodley, J. D., Chornesky, E. A., Clifford, P. A., Jackson, J. B. C., Kaufman, L. S., Knowlton, N., Lang, J. C., Pearson, M. P., Porter, J. W., Rooney, M. C. et al. (1981). Hurricane Allen's impact on Jamaican coral reefs. *Science* **214**, 749-755.

Zakai, D., Levy, O. and Chadwick-Furman, N. E. (2000). Experimental fragmentation reduces sexual reproductive output by the reef-building coral *Pocillopora damicornis*. *Coral Reefs* **19**, 185-188.

Appendices

Appendix 1. Model software

The model was programmed in Visual Basic Professional Edition 6.0. The reason for this was primarily because of the high resolution graphics that are relatively straightforward to code for and display. This was in order to view the model screen output as the model ran. The second reason for using Visual Basic was because of the familiar windows format for applications. This, together with the fact that it is object orientated (the objects are ready made, some with pre-written routines) thereby substantially reduced time to create complex programs with user-friendly interfaces. These features may compromise runtime to a certain extent, but as code can be compiled in C for fast execution, it was considered a reasonable trade-off. A final advantage of this language is that it is easy to learn; I wrote the body of the software in the first six months of this PhD, having no prior programming experience.



The above picture shows the model-user interface with a range of settings that can be adjusted as required. It is hoped that this software can be further extended in the future and later become available for distribution.

Appendix 2. Species attribute sources

2.1 Growth rate

Rates of growth for modelled coral species for corals growth at different depth ranges

Species	0-5 m	6-15 m	16-25 m	>25 m	Source	Rate used
Montastraea cavernosa		0.5	0.8	0.5	e	0.5
	0.5	0.5	0.5		h	
	0.4	0.4			i	
	0.3	0.3			j	
Stephanocoenia michellenii						1
Agaricia agaricites	1.1				A	2
			2.4		B	
Eusmilia fastigiata						1
Meandrina meandrites						2
Montastraea annularis	0.6				a	1
		2.4			d	
	0.9	1.0	0.5	0.2	f	
		0.6		0.2	g	
	0.7	0.8			c	
		0.7			b	
	0.7	0.9	0.2	0.2	e	
	0.7	0.7			h	
	0.5	0.5			i	
	1.3	1.1			j	
Colpophyllia natans	1.0	0.7	0.4	0.2	e	1
Porites astreoides	0.9				a	0.5
	0.4	0.3			c	
	0.4	0.4	0.3	0.2	e	
	0.5	0.5			h	
Madracus asperula		2.4			d	2
Siderastrea siderea	0.3	0.8	0.4		e	0.8

[a] Vaughan (1915) Florida in (Huston, 1985)
[b] Bak (1976) Curacao
[c] Gladfelter et al. (1978) Virgin Islands
[d] Lewis et al. (1968) Jamaica
[e] (Huston, 1985) Jamaica
[f] Baker & Weber (1975) Virgin Islands
[g] Dustan (1975, 1979) Jamaica
[h] Highsmith et al. (1983) Belize
[i] Weber & White (1977) Florida, Belize
[j] Bak & Criens (1981) Curacao

2.2.1 Species composition of recruits

Percentage newly settled coral larvae by species

Species group	A	b	C	d	e	f	Mean %
Agaricia spp.	81	60	22	68	34	34.6	49.9
Porites astreoides	8	3	41	0	0	0	8.7
Porites spp.	2	14	16	11	0	44.2	14.5
Stephanocoenia michelli	0	5	0	1	0	0	1.0
Montastraea annularis	2	0	11	0	0	0	2.2
Siderastrea spp.	0	0	7	0	0	0	1.2
Madracis decactis	0	0	0	20	0	0	3.3
Others	7	4	0	0	8	0	3.2

a (Rylaarsdam, 1983), Jamaica 11-14m, substratum: trimmed *A. cervicornis* branches
b (Rylaarsdam, 1983), Jamaica 11-14m, substratum: artificially cleared substratum
c (Tomascik, 1991), Barbados 2-4m, substratum: terracotta tiles
d (Rogers et al., 1984) USVI 9-37m, substratum: slabs of *Acropora palmata*
e (Hughes, 1985) Jamaica 10-20m, substratum: artificially cleared substratum
f Source uncertain

2.2.2 Number of recruits

Coral recruitment rates per m^2 for various locations (after (Smith, 1992))

Location	Spat per $m^{-2} yr^{-1}$	Source
Bermuda	160	Smith (1985)
Bermuda	15	Smith (1988)
Bermuda*	15	(Smith, 1992)
St Croix	6	(Rogers et al., 1984)
Jamaica	60	(Rylaarsdam, 1983)
Jamaica	378	(Sammarco, 1980)
Jamaica*	20	(Hughes, 1985)
Gulf of Mexico	123	(Baggitt and Bright, 1985)
Average	97.13	

* All studies used removable substrata except those annotated, which used high-resolution photoquadrats

2.2.3 Mode of larval development

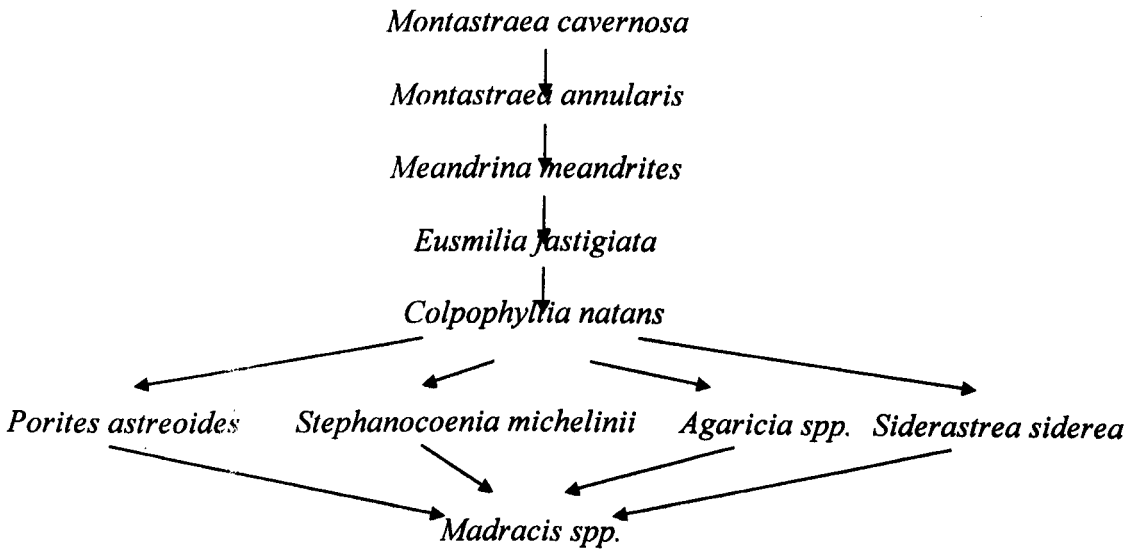
Mode of larval development for selected Caribbean coral species

Species	Gender	Embryonic development
Montastraea cavernosa	Dioecious[b]	Planktonic[ab]
Stephanocoenia michelinii		Planktonic[d]
Agaricia agaricites	?	Brooded[ab]
Eusmilia fastigiata	?	Brooded[c]
Meandrina meandrites		Planktonic[c]
Montastraea annularis	Hermaphrodite[b]	Planktonic[ab]
Colpophyllia natans	?	Planktonic[d]
Porites astreoides	Hermaphrodite[b]	Brooded[ab]
Madracis spp.		?
Siderastrea siderea	Dioecious[b]	Planktonic[ab]

a (Chiappone and Sullivan, 1996) Florida Reef Tract
b (Szmant, 1986) Puerto Rico
c coral list – get ref.
d Veron (Chris Schelton pers comm.)

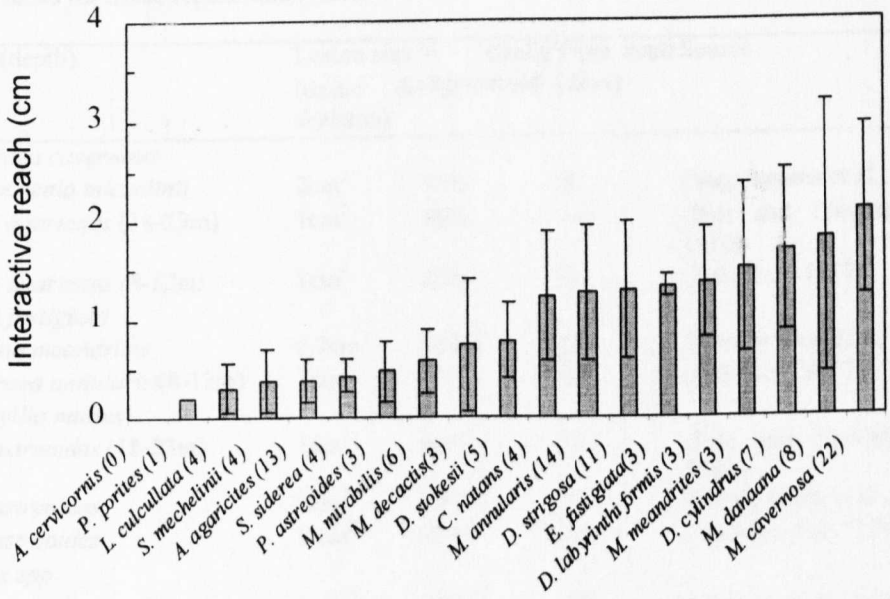
2.3. Spatial competition

2.3.1. Competitive hierarchy



Hierarchy of competitive proficiency derived from observations taken in Utila, Bay Islands, Honduras (August 1999).

2.3.2. Interactive reach



Interactive reach of interacting corals, with number of observations in parentheses. Observations taken in Utila, Bay Islands, Honduras (August 1999).

2.4. Differential mortality probability

2.4.1. Colony size

Colony sizes from two sites in Curacao (given as geometric mean, cm^2), with mean size and rank (Meesters et al., 2001).

Species group	Cornelisbay	Seaquarium	Mean	Rank
M. cavernosa	769	823	796	4
S. michelinii				3
Agaricia spp.	42	50	46	1
E. fastigiata	113	72	92.5	2
M. meandrites	105	29	67	2
M. annularis	3062	1876	2469	5
C. natans	2	269	254.5	3
P. astreoides	58	29	43.5	1
Madracis spp.				2
S. siderea	2	407	345	3

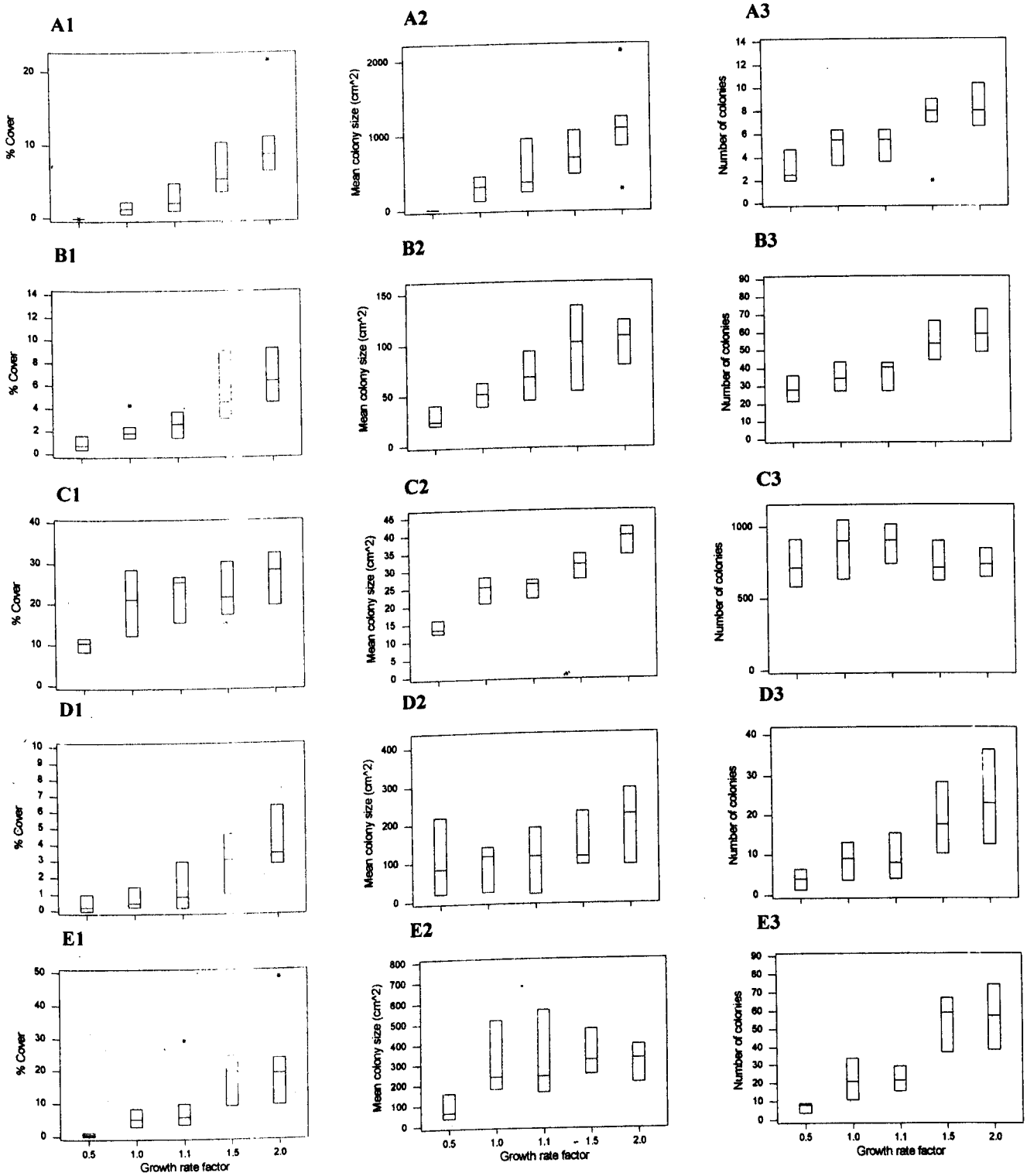
2.4.2. Tissue regeneration rates

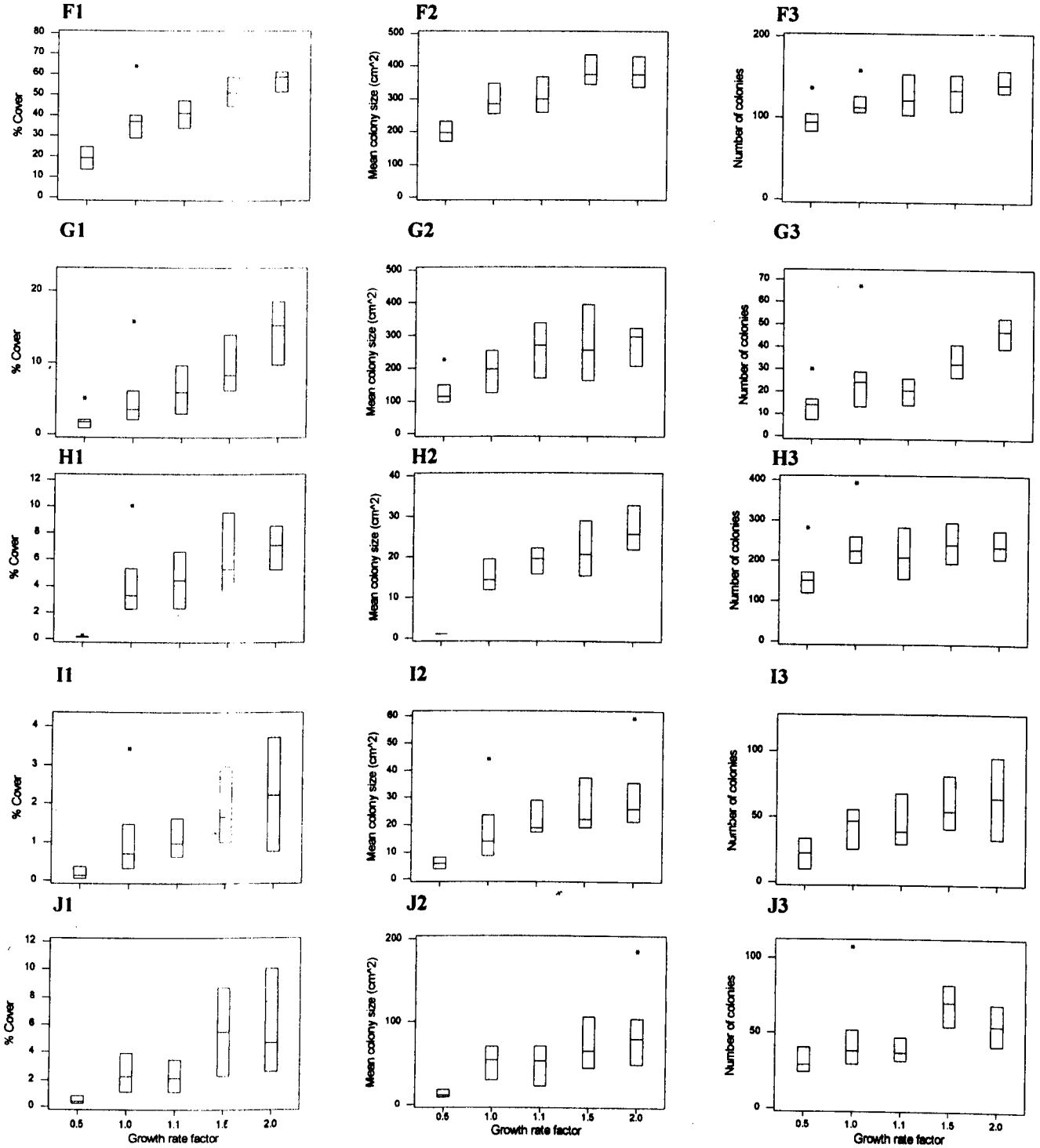
Relative ranks for tissue regeneration rates.

Species (depth)	Lesion size (tissue & skeleton)	% totally regenerated	Time scale (days)	Source	Rank
Montastraea cavernosa					2
Stephanocoenia michelinii	$2cm^2$	90%	30	(Nagelkerken et al., 1999)	3
Agaricia agaricites (18-23m)	$1cm^2$	48%	140	(Bak and Steward van Es, 1980)	1
Agaricia agaricites (8-12m)	$1cm^2$	20%	80	(Bak et al., 1977)	
Eusmilia fastigiata					3
Meandrina meandrites	$0.7cm^2$	100%	16	(Meesters and Bak, 1993)	5
Montastraea annularis (8-12m)	$1cm^2$	70%	80	(Bak et al., 1977)	3
Colpophyllia natans					3
Porites astreoides (18-23m)	$1cm^2$	64%	140	(Bak and Steward van Es, 1980)	4
Porites astreoides	$2cm^2$	90%	50	(Nagelkerken et al., 1999)	
Porites astreoides	$5\ cm^2$	60%	660	(Guzman et al., 1994)	
Madracis spp.					3
Siderastrea siderea	$5\ cm^2$	35%	660	(Guzman et al., 1994)	1

Appendix 3. Sensitivity Testing

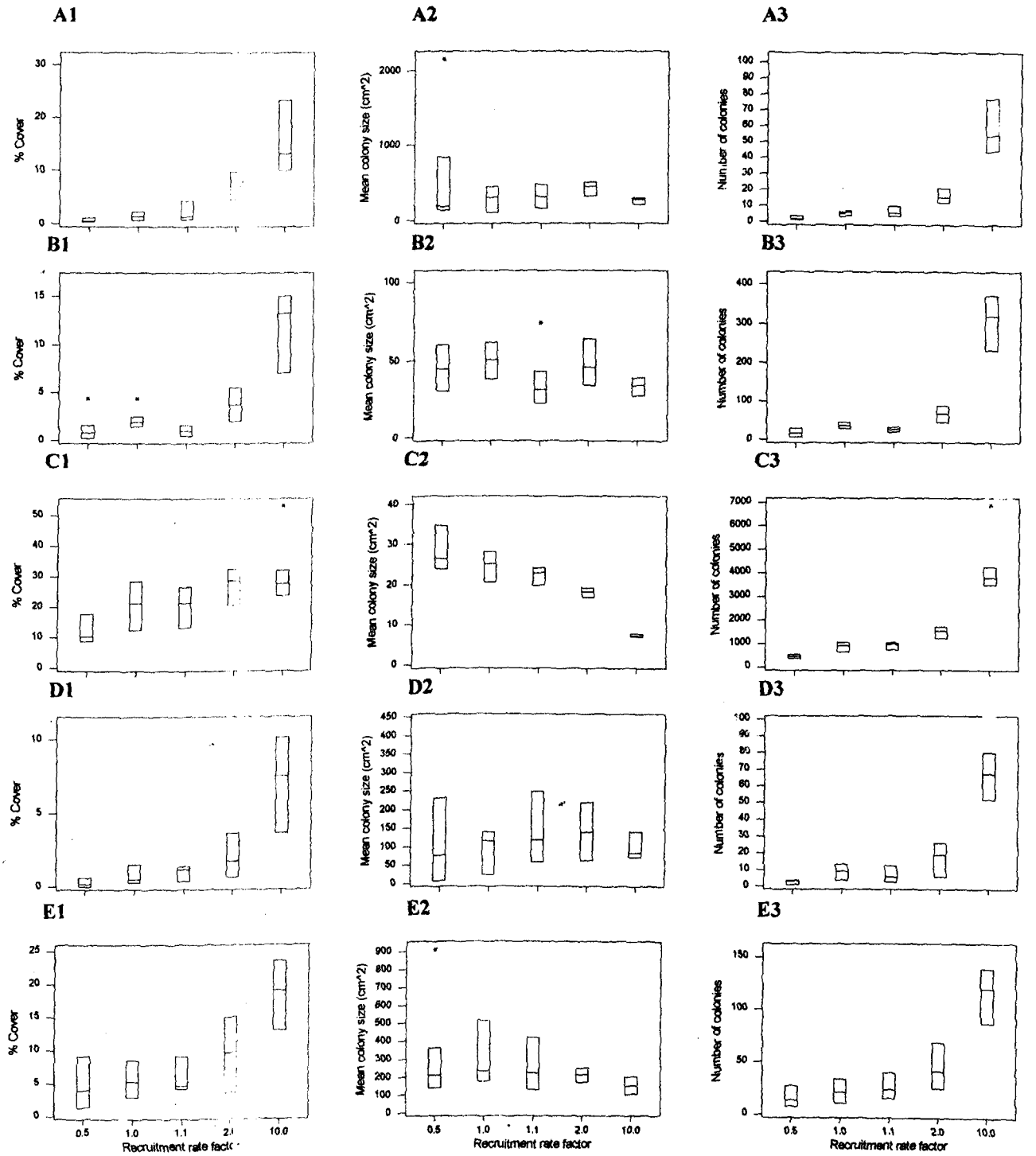
3.1. Effect of variations in growth

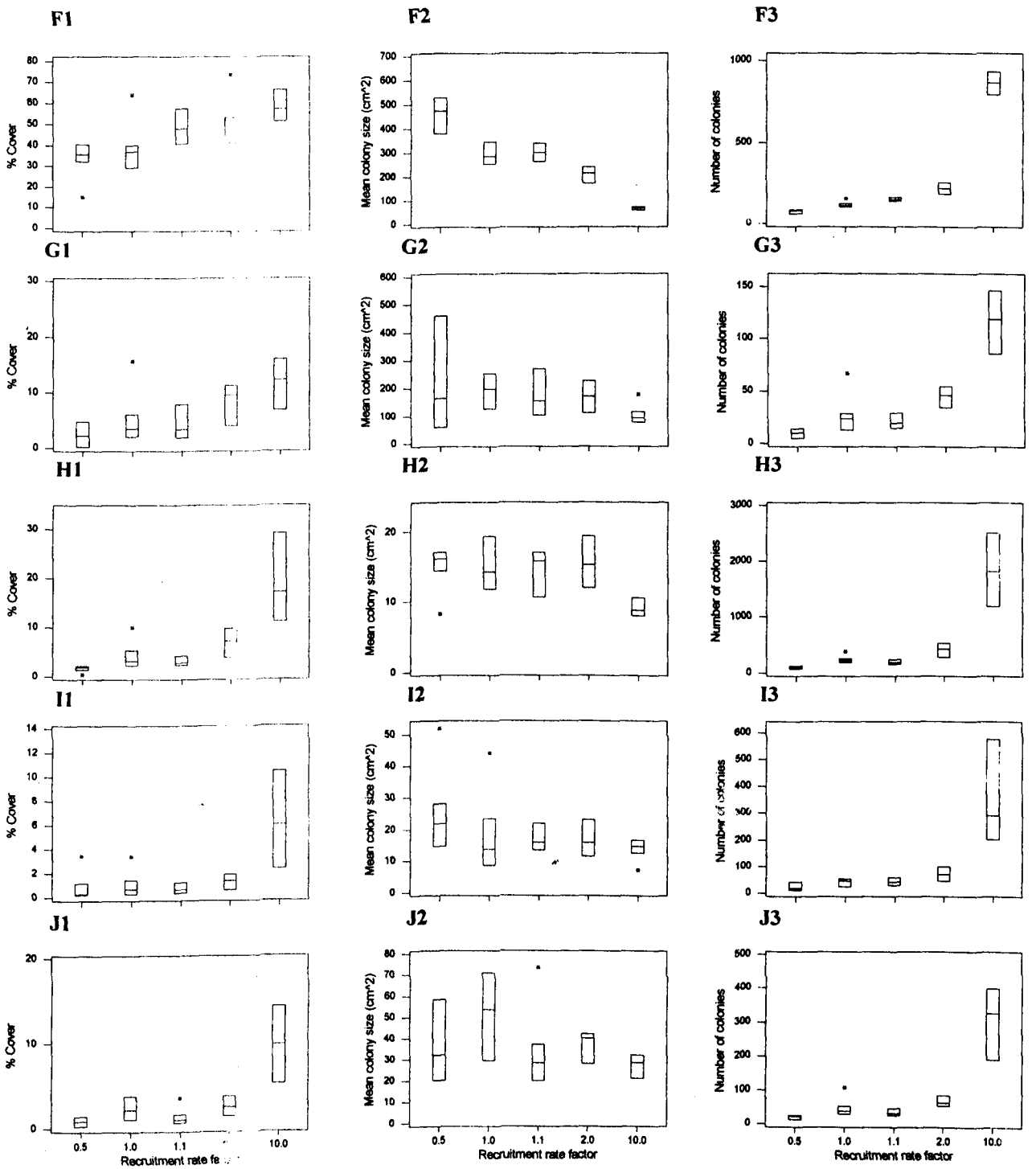




Effect of variations in growth rate on modelled corals. A *Montastraea cavernosa*, B *Stephanocoenia michelinii*, C *Agaricia* sp., D *Eusmilia fastigiata*, E *Meandrina meandrites*, F *Montastraea annularis*, G *Colpophyllia natans*, H *Porites astreoides*, I *Madracis* spp. and J *Siderastrea siderea*. For each species group: 1 Percent cover, 2 Mean colony size (planar area, cm^2) and 3 Number of colonies, n = 10 replicates. Boxes indicate 95% confidence intervals transected by the median, * are outliers, n = 10 replicates.

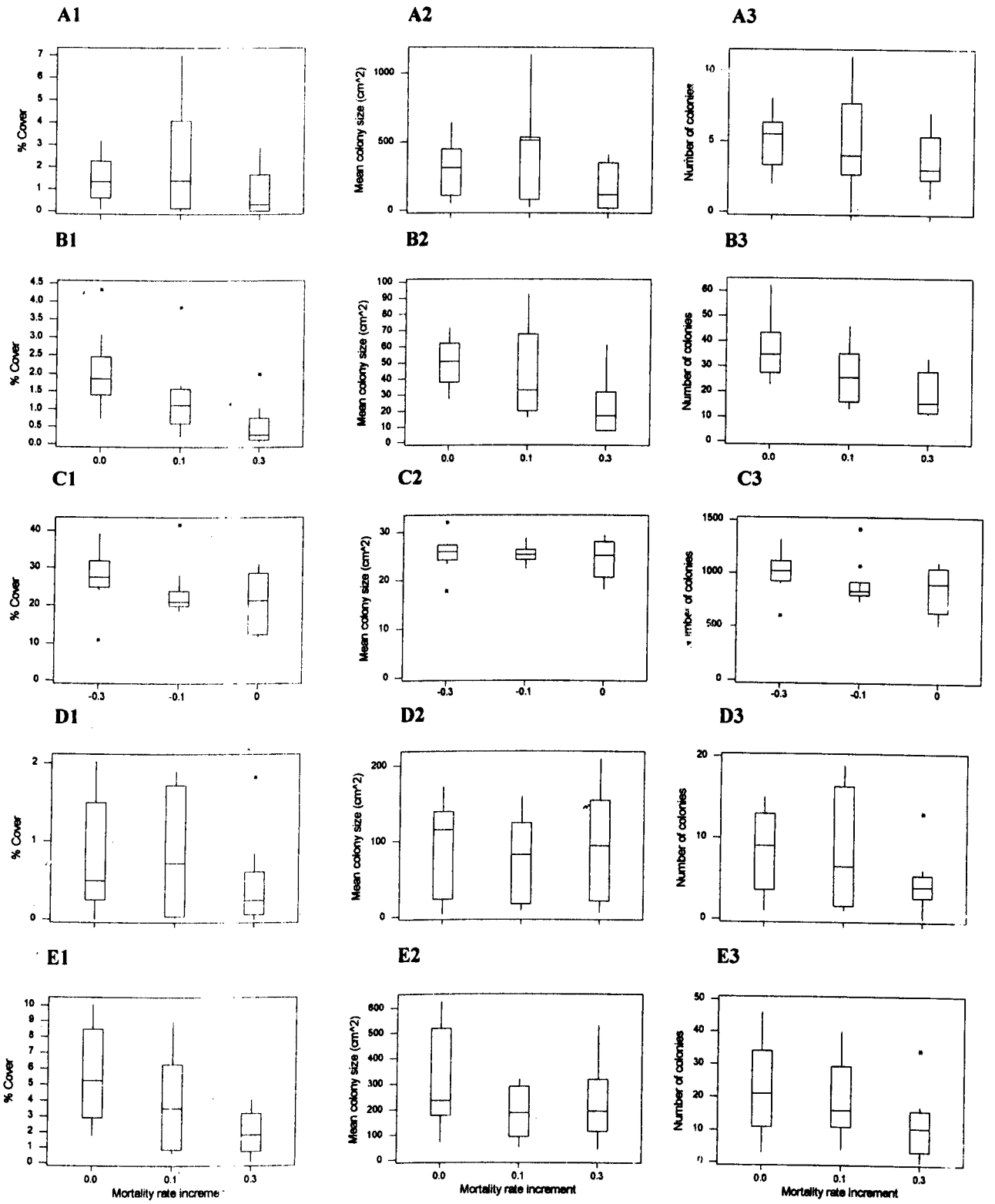
3.2. Effect of variations in recruitment

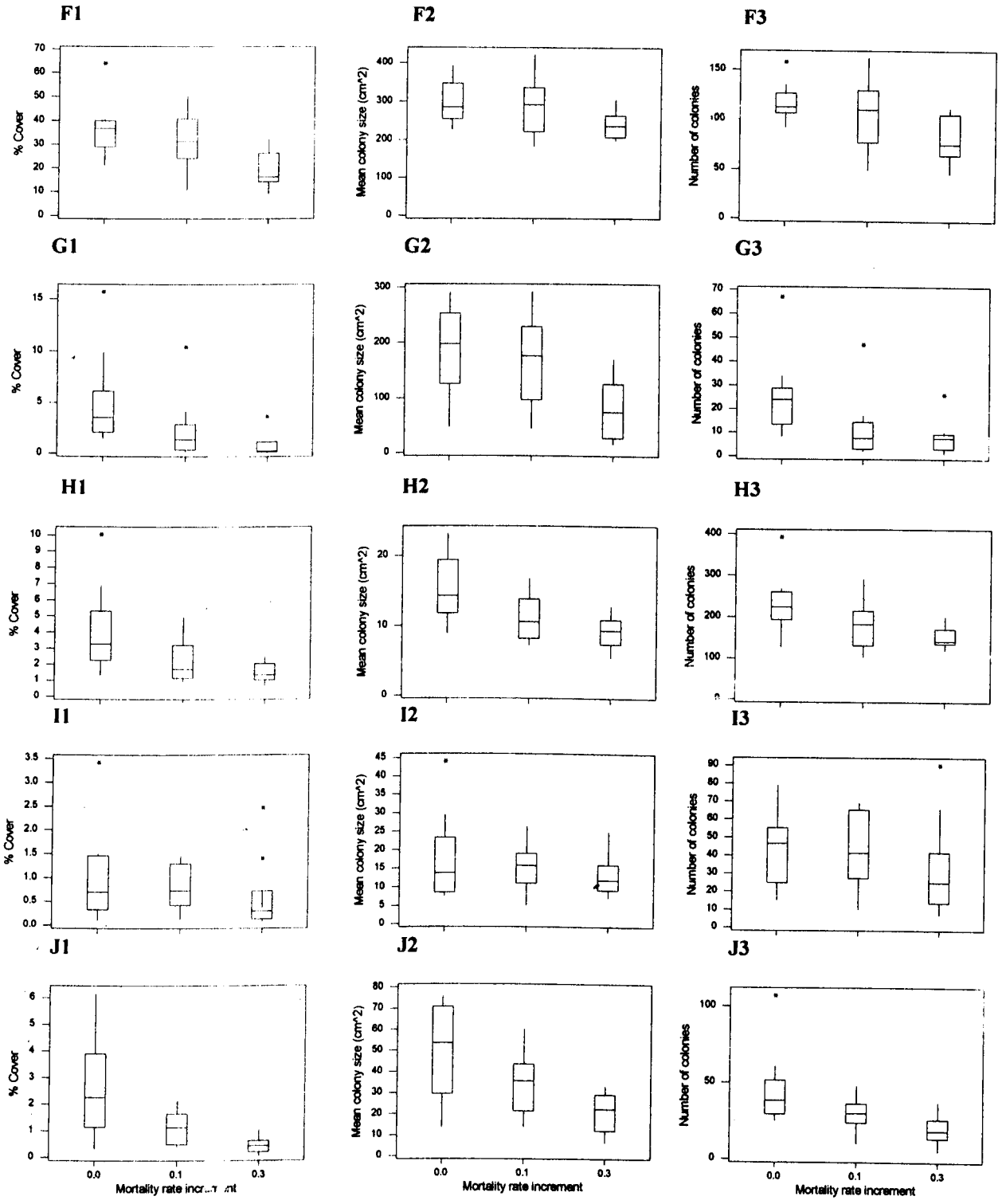




Effect of variations in recruitment rate on modelled corals. A *Montastraea cavernosa*, B *Stephanocoenia michelinii*, C *Agaricia spp.*, D *Eusmilia fastigiata*, E *Meandrina meandrites*, F *Montastraea annularis*, G *Colpophyllia natans*, H *Porites astreoides*, I *Madracis spp.* and J *Siderastrea siderea*. For each species group: 1 Percent cover, 2 Mean colony size (planar area, cm^2) and 3 Number of colonies, n = 10 replicates. Boxes indicate 95% confidence intervals transected by the median, * are outliers, n = 10 replicates.

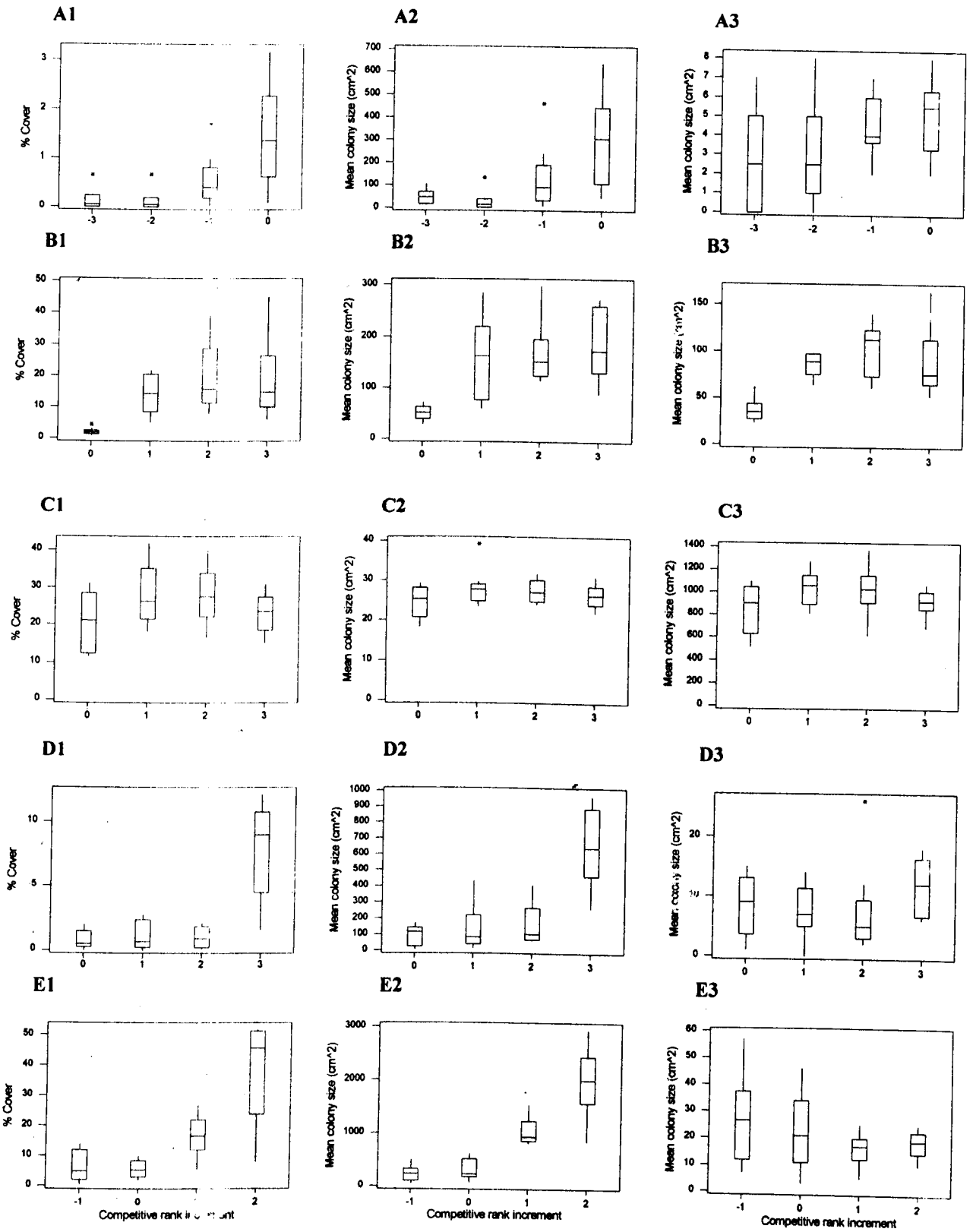
3.3. Effect of variations in differential mortality probability

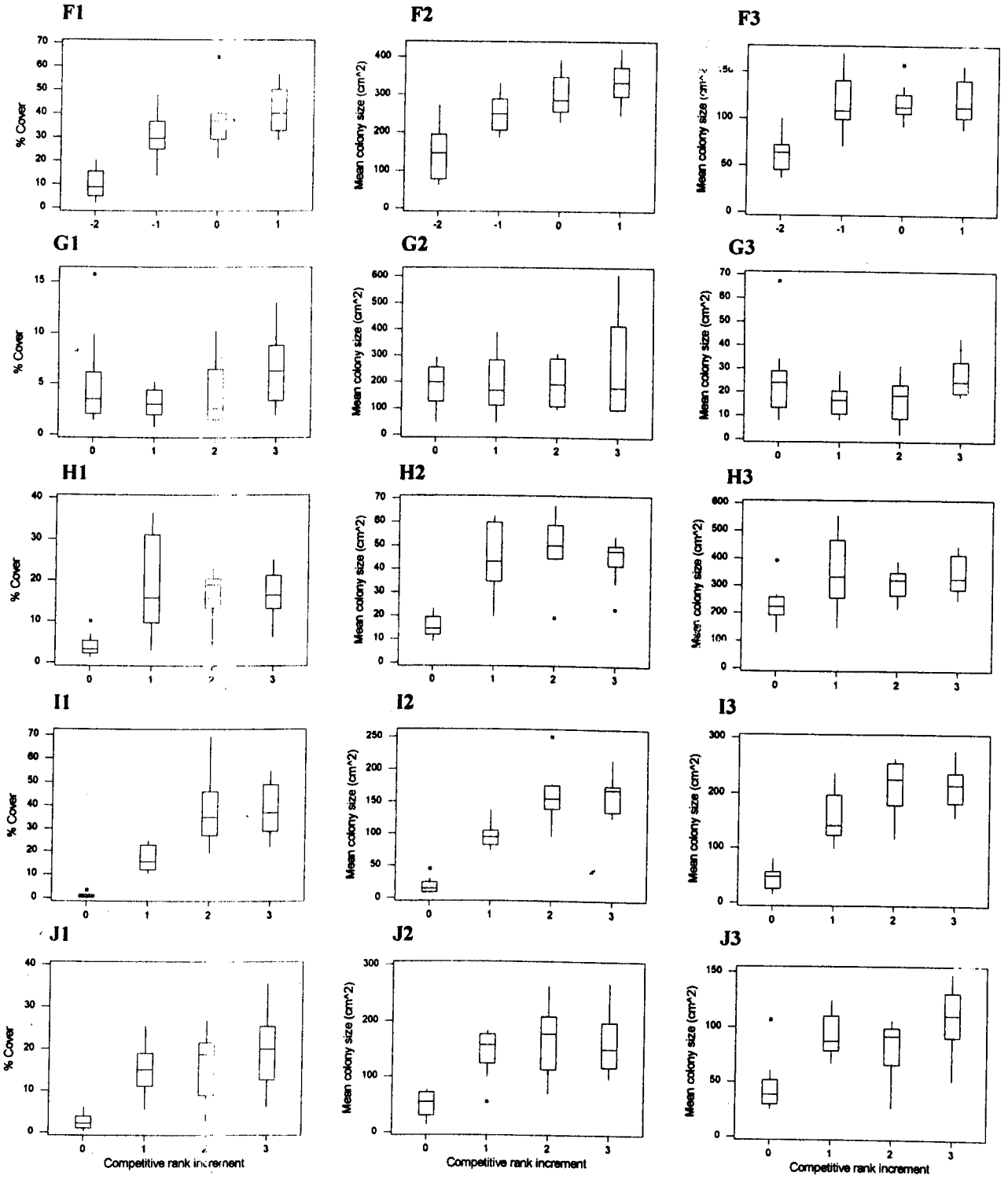




Effect of variations in relative mortality probability on modelled corals. A *Montastraea cavernosa*, B *Stephanocoenia michelinii*, C *Agaricia spp.*, D *Eusmilia fastigiata*, E *Meandrina meandrites*, F *Montastraea annularis*, G *Colpophyllia natans*, H *Porites astreoides*, I *Madracis spp.* and J *Siderastrea siderea*. For each species group: 1 Percent cover, 2 Mean colony size (planar area, cm^2) and 3 Number of colonies, n = 10 replicates. Boxes indicate 95% confidence intervals transected by the median, * are outliers, n = 10 replicates.

3.4. Effect of variations in aggressive rank





Effect of variations in competitive rank variation on modelled corals. A *Montastraea cavernosa*, B *Stephanocoenia michelinii*, C *Agaricia spp.*, D *Eusmilia fastigiata*, E *Meandrina meandrites*, F *Montastraea annularis*, G *Colpophyllia natans*, H *Porites astreoides*, I *Madracis spp.* and J *Siderastrea siderea*. For each species group: 1 Percent cover, 2 Mean colony size (planar area, cm^2) and 3 Number of colonies, n = 10 replicates. Boxes indicate 95% confidence intervals transected by the median, * are outliers, n = 10 replicates.

Appendix 4. Global climate model characteristics

4.1. HadCM3GGa

These models and general circulation models (GCM) from other modelling centres have required flux corrections to be applied to prevent the simulated climate from drifting as a result of an imbalance between implied and actual ocean heat transports. HadCM3 is the first of a new generation of coupled atmospheric GCMs that do not require flux corrections.

4.2. GCM Model characteristics

The atmospheric model used is the HadAM3 version of the UK Met. Office's unified forecast and climate model with a horizontal resolution of 2.5 x 3.75 degrees and 19 vertical levels. The ocean component is a 20 level version of the model with a spatial resolution of 1.25 x 1.25 degrees, thus resulting in six ocean grid cells to one atmosphere grid cell. The vertical levels are distributed to produce higher resolution spacing nearer the surface. The coastline of the model is at a resolution of 2.5 x 3.75 degrees, allowing for enhanced coupling between atmosphere and ocean components.

4.3. GCM model performance

The HadCM3 coupled model has an improved sea-surface temperature (SST) and sea-ice climatology compared to earlier generations of the model in which flux corrections were required. The other major improvements in performance include:

a) In coupled mode, the ocean model maintains poleward heat transport, thus producing a self-consistent system and negating the need for flux correction.

b) The SST pattern in HadCM3 stabilises after only a few decades and the thermohaline circulation is stable.

c) The drift of the model as represented by the SST is less than 0.2 °C over a 400 year period.

4.4. Specific GCM model integration

From the various model integrations, the greenhouse gas (GGa1) data were used for this work. HadCM3GGa1 was forced using the historical increase in the individual

greenhouse gases (GHGs) from 1860-1990, and then using individual increases in GHGs as described in the IS95a (a 1% per year compound rise in radiative forcing) emissions scenario. Tropospheric ozone was not included, as its geographical distribution is not specified in IS95a. The forcing from 1990-2100 is based upon the IS95a emissions scenario, however it is slightly less, IS95a assumes a forcing of 4.39 Wm^2 on CO2 doubling whereas HadCM3 produces a forcing of 3.74 Wm^2. HadCM3 integrations with SRES emissions scenarios (IPCC, 2000) were not used, in order to keep the experimental design simple.